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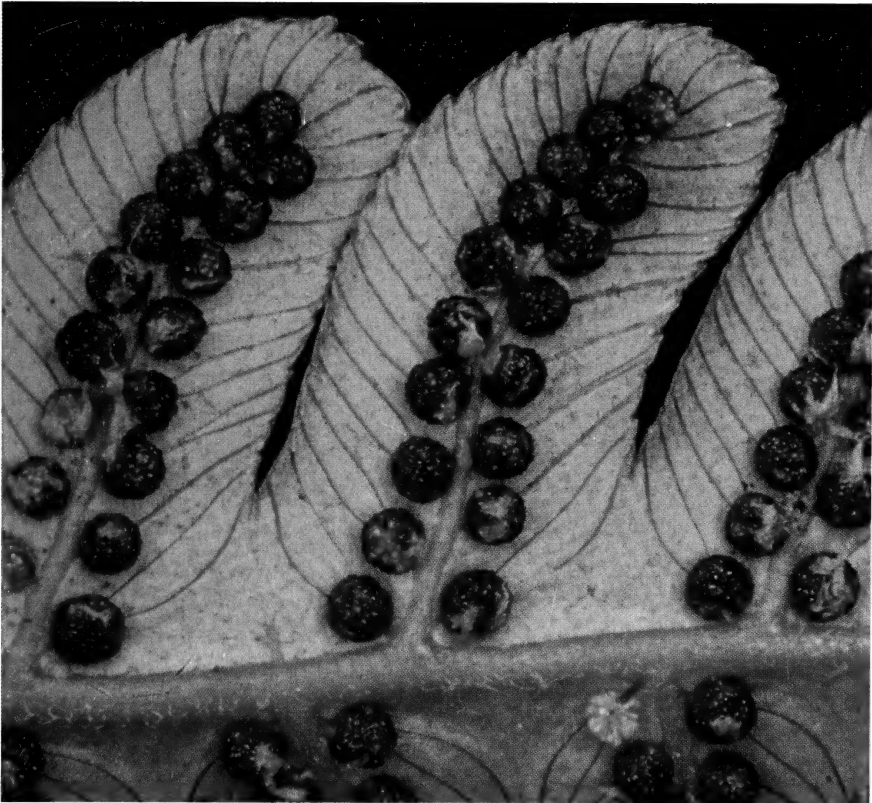
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## New Additions of Scaly Tree Ferns (Cyatheaceae) to the Flora of Colombia

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**ABSTRACT.**—As the result of ongoing studies of the fern flora of Colombia, we here present 14 taxa of the scaly tree ferns (Cyatheaceae) that are either new to science (*Cyathea andaquiensis*, *C. callejasii*, *C. cardenasii*, *C. catenata*, *C. coloradoana*, *C. kessleriana*, *C. pacis*, *C. pholidota*, *C. rengifoii*, *C. rodriguezii*, *C. tejedoris*, *C. toroi*) or newly recognized (*Cyathea boconensis*). For *Alsophila crassa*, the new name *C. clandestina* is chosen and an updated description is given.

**KEY WORDS.**—Andes, biogeography, conservation, Neotropics, South America

Colombia is one of the most diverse countries in South America regarding biotopes (Olson and Dinerstein, 1998), biogeographic regions (Sánchez-Cuervo *et al.*, 2012) and species richness (Kier *et al.*, 2009). Its fame for harboring the highest number of bird species has long been established (Hilty and Brown, 1986), and its top position for species richness of other taxonomic groups often predicted (Kier *et al.*, 2009). Since the recent solution of inner political conflicts that for the past 40 years had withheld scientific exploration of most rural parts (Sánchez-Cuervo and Aide, 2013), local and international scientists are gradually gaining access to the biodiversity of areas spared the detrimental impact of civilization, and discovering new species of sometimes strikingly distinctive appearances (Cuervo *et al.*, 2005; Defler, Bueno, and García, 2010; Lara *et al.*, 2012; Mantilla-Melluk and Baker, 2006; Moncada and Luecking, 2012; Roman-Valencia *et al.*, 2010; Vasco, 2006; Veneagas, González, and Puerta, 2012). This includes also samples of scaly tree ferns of the family Cyatheaceae unassignable to species (Rojas and Tejedor, 2016; Tejedor *et al.*, 2017). This still comes as a surprise because this showy plant group, like

orchids or palms, has been frequently collected in this country since the first botanical explorations during the Spanish colonial era (Bonpland *et al.*, 1815; Humboldt and Bonpland, 1807; Karsten, 1856, 1860, 1869; Lack, 2003; Mutis, 1967) and was considered relatively well understood (Barrington, 1978; Murillo and Murillo, 2003; Tryon, 1976).

The scaly tree ferns have become a high priority focus for Colombian scientists because these conspicuous plants are listed as endangered in the index of CITES species (CITES, 2017) in order to restrict and control their trade. This protective measure is necessary because tree fern trunks of Cyatheaceae and Dicksoniaceae with their fibrous root mantle are locally used for making special flowerpots and substrates for epiphytic plants, such as orchids (Eleutério and Pérez-Salicrup, 2006). The few available demographic studies on tree ferns (Ramírez-Valencia, Sanín, and Álvarez-Mejía, 2009; Seiler, 1981, 1995) indicate that the preferably harvested species need about two decades to reach fertility and many more to develop a trunk that justifies harvesting. Adding the negative influence of general habitat deterioration by humans, many tree ferns are probably endangered in the wild but the exact status of their populations is currently unknown. For this reason, the Instituto Amazónico de Investigaciones Científicas SINCHI under auspices of the Colombian Ministerio de Ambiente is conducting a nationwide assessment of the distribution and abundance of tree ferns in order to categorize their threats and make suggestions for location and extension of new protected areas. When SINCHI asked for our taxonomic expertise in order to accelerate this assessment, offering in return logistic help with collection permits and specimen export, we gladly accepted. Our main focus was on the re-collection of the known species for phylogenetic studies and the geographic assessment in Colombia, but with the combined fresh experience from the field and the Colombian herbaria, many taxa of tree ferns became easily recognizable that should be treated as proper species (Noben *et al.*, 2018). Here, we present the first taxonomic novelties in the genus *Cyathea*.

#### MATERIALS AND METHODS

We studied specimens in the largest Colombian herbaria: CAUP, COAH, COL, CUCV, FMB, HUA, JAUM, MEDEL, TULV, VALLE (Thiers, 2016). Other collections were consulted from AAU, B, BM, F, GOET, K, L, M, MO, P, STU, UC, US, W, and Z for types and comparative material. The authors took field trips to all ecoregions of Colombia, and type localities of species described from Colombia were visited as far as possible. Specimens of the authors' collections are mainly deposited at HUA and COAH, with duplicates deposited at BONN and Z. Terminology follows Lellinger (2002) and Lehnert (2011).

#### RESULTS & DISCUSSION

We here present 14 newly recognized species of the scaly tree ferns (Cyatheaceae), twelve are new to science (*Cyathea andaquiensis* Lehnert,



F.Giraldo & W.Rodríguez *sp.nov.*, *Cyathea callejasii* Lehnert, F.Giraldo & A.Tejedor *sp.nov.*, *Cyathea cardenasii* Lehnert, F.Giraldo & W.Rodríguez *sp.nov.*, *Cyathea catenata* Lehnert, F.Giraldo & W.Rodríguez *sp.nov.*, *Cyathea coloradoana* Lehnert, F.Giraldo & W.Rodríguez *sp.nov.*, *Cyathea kessleriana* Lehnert, F.Giraldo & A.Tejedor, *sp.nov.*, *Cyathea pacis* F.Giraldo, W.Rodríguez & A.Tejedor *sp.nov.*, *Cyathea pholidota* Lehnert, F.Giraldo & A.Tejedor, *sp.nov.*, *Cyathea rengifoii* Lehnert, F.Giraldo & A.Tejedor *sp.nov.*, *Cyathea rodriguezii* Lehnert & F.Giraldo, *sp.nov.*, *Cyathea tejedoris* Lehnert, F.Giraldo & W.Rodríguez, *sp.nov.*, and *Cyathea toroi* Lehnert, F.Giraldo & A.Tejedor *sp.nov.*) and two are reinstated (*Cyathea boconensis* H.Karst., *Cyathea clandestina* Lehnert, F.Giraldo & A.Tejedor *nom. nov.*).

In most of these species, we observed structures at the joints between rachises and costae that could represent foliar nectaries (White and Turner, 2012). These are found below the pneumathodes, if pneumathodes occur in the species, and are visible as differently colored parts of the epidermis, either as green, shiny areas in fresh material or darkened (sometimes also wrinkly) spots in dried material. We follow the interpretation of White and Turner (2012) and label them here as foliar nectaries, albeit tentatively, because we have not observed visiting ants or other insects in the field. Furthermore, it appears that these structures lose their function in older fronds, where they are often dried up, dull, and less visible compared to those on younger fronds.

Most of the newly recognized species occur either in the Chocó region (Provs. Chocó, Risaralda, Valle de Cauca) or in the northern part of the Colombian Cordilleras facing the Caribbean (Provs. Antioquia, Santander). All species treated here belong to *Cyathea* in the strict sense, and mostly to the clades of *C. divergens* and *C. gibbosa* sensu Korall *et al.* (2007) and Lehnert *et al.*, (unpubl. data).

#### TAXONOMIC TREATMENT

##### New Species

1. ***Cyathea andaquiensis*** Lehnert, F.Giraldo & W.Rodríguez, ***sp. nov.*** Type: COLOMBIA. Caquetá: Municipio Belén de Los Andaquies, Parque Natural Municipal Andaqui, cabeceras del Río Pescado 01°41'52.6"N, 75°54'15.9"W, 1608 m, 25 Jan 2017, N. Castaño-A., D. Cardenas, J. Betancur, A. Barona, N. Marin, E. Paky, J. Navarro, O. Cerquera, A. Valencia, M. Rojas, B. Rojas, D.J. Jaimes, L.C. Luna, H. Muñoz & D. Osorio 8827 (holotype: COAH-96598/-96596/-96623!, isotype: COL-0004565525/-000456604/-000456856!). Fig. 1.

Trunks erect, to 1 m tall, 6–8 cm diam.; adventitious buds not reported. Petioles to 40 cm long, strongly aculeate, with prickles to 3 mm long, brown to dark brown; without adventitious (aphlebioid) pinnae at the petiole bases; scurf absent; petioles adaxially hairy down to their bases, abaxially hairy at least in upper parts, hairs to 2 mm long, catenate, flaccid, tortuous, whitish to pale brown; petiole scales lanceate, 18–25 × 2–3 mm, their tips straight, weakly

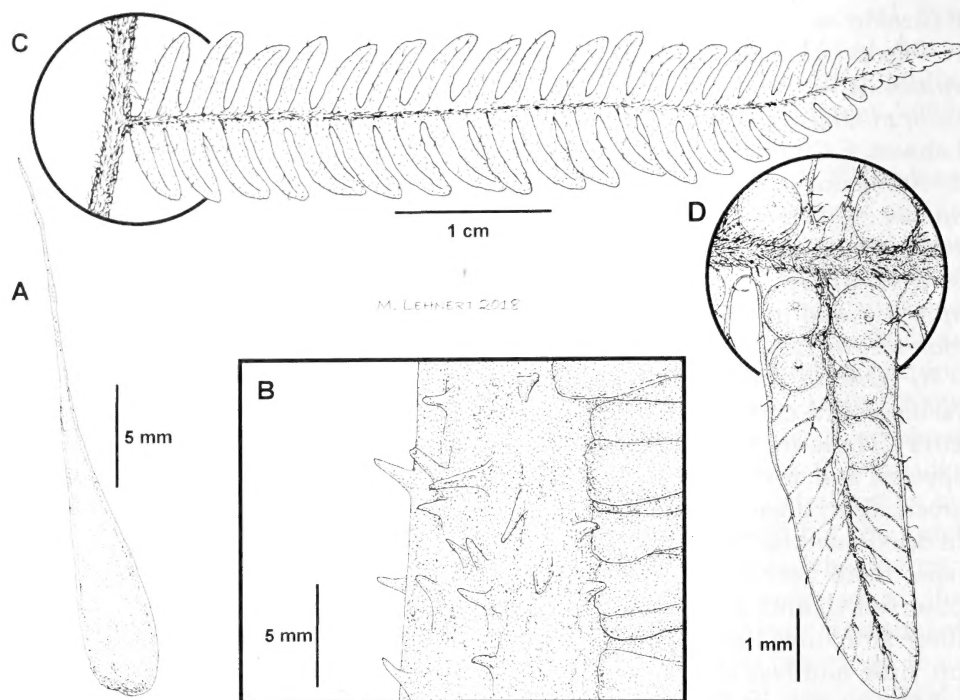


FIG. 1. *Cyathea andaquiensis*. A. Petiole scale. B. Petiole with scales. C. Pinnule, adaxially. D. Segment abaxially, showing the complete sphaeropteroid indusia (all drawn from *Colorado 651*, HUA).

twisted, lustrous, concolorous to weakly concordantly bicolorous, the brown to dark brown center transitioning into the brown to yellowish-brown margins. Fronds to 140 cm long, held  $\pm$  stiffly erect. Laminae to  $100 \times 40$  cm, bipinnate-pinnatifid to -pinnatisect, chartaceous, widest at the middle, apices gradually reduced; dark green adaxially, blackish when dried, dull olive-green abaxially. Pinnae to 20 cm long, ca. 8–9 pairs per frond, sessile to subsessile with stalks to 0.5 cm, distally narrowly green alate between the segments. Frond axes (rachis, costae, costules) dark reddish brown, adaxially darker than abaxially, abundantly hairy, hairs to 2 mm long, tan to orange-brown, adaxially very dense, antrorsely curved to appressed, abaxially less dense, more spreading, abaxially also with flat linear-lanceate scales  $2\text{--}12 \times 1\text{--}3$  mm, orange-brown or with whitish margins or bases, mainly in the axils of the axes; rachises abaxially aculeate, costae muricate, costules inermous; junctures of costae and rachises abaxially weakly swollen, each with a planar elliptic pneumathode to  $3 \times 1\text{--}2$  mm, dark brown, inconspicuous, with blackened area below in dried specimens. Pinnules to  $5.5 \times 1.0\text{--}1.2$  cm, sessile, mostly alternate, ca. 1 cm between the costules, linear-lanceate, cuneate to rounded at base, tapering from beyond the middle to acute to attenuate tips; segments to  $6 \times 1.5\text{--}2.0$  mm, weakly ascending, weakly falcate towards the tip, with crenulate to subentire

margins and obtuse tips; with a small blackish elliptic pneumathode at the base of the costules; basal segments alternately placed, approximate, sinuses 0.5–1.0 mm wide, acute to obtuse; sterile and fertile pinnules identical. Veins adaxially with white to tan, erect, straight to curved, multicellular hairs 0.5–1.0 mm long, the longest ones on the midveins; abaxially with many white, tortuous multicellular hairs 0.5–1.0 mm long on and between the veins, sometimes on the veins intermixed with small appressed trichomidia to 0.2 mm long; costules and midveins abaxially yellowish to carneous, planar to weakly raised, with orange-brown to brown, flat squamules to 1.0 mm long with elongated tips and fimbriate to dissected margins, pale bullate squamules few distally on midveins; lateral veins flat, dark green to blackish; sterile veins forked or simple, fertile veins forked. Sori 0.6–0.8 mm diam., each with ca. 15 sporangia,  $\pm$  medial to subproximal, indusia sphaeropteroid with umbo, tan, translucent; receptacles globose, 0.2 mm diam, paraphyses few, hyaline, tan, of the same length as sporangia (0.3 mm). Spores not examined.

*Etymology*.—The epithet refers to the type locality in the Municipio de Belén de los Andaquíes, to raise awareness of the threat of habitat destruction by illegal logging in that area.

*Distribution and Habitat*.—Southeastern Colombia (Caquetá) in wet montane forests at 1608 m.

*Cyathea andaquiensis* belongs to the group of sphaeropteroid-indusiate species of *Cyathea*, such as *C. squamipes* H.Karst. and *C. delgadii* Pohl ex Sternb., to which it bears some superficial resemblance. It stands out by its dense indument of pale soft flaccid hairs that form a woolly cover abaxially on costae and costules. In *C. delgadii* and *C. squamipes*, the hairs on costae and costules are less dense and mostly spreading or arching. The only sphaeropteroid-indusiate species that resemble *C. andaquiensis* regarding the dense soft hair are *C. harrisii* Underw. of Jamaica and Hispaniola and *C. chimaera* Lehnert & A.Tejedor of the Huancabamba region: *Cyathea harrisii* usually has larger pinnules with clear stalks to 4 mm, and *C. chimaera* has inermous petioles and rachises (vs. aculeate in *C. andaquiensis*), blunt pinnules (vs. attenuate) and reduced scale margins (vs. differentiated margins well-developed).

Little is known about the ecology of *Cyathea andaquiensis*. It occurred on a steep slope covered in wet forest with a canopy height of 16 m and an abundance of the palm *Dictyocaryum lamarckianum* H.Wendl. The presence of dense undergrowth suggests a relatively open forest structure. This would explain also the short trunk of the fertile plant of the type collection and the erect position of the fronds, which we reconstructed from the stiff, straight rachis and the acute insertion to the trunk, as indicated by the form of the petiole abscission layer.

2. *Cyathea callejasii* Lehnert, F.Giraldo & A.Tejedor, *sp. nov.* Type: COLOMBIA. Antioquia: Municipio Frontino, Vereda El Guayabo, Corregimiento Nutibara, 06°41'20.5"N, 76°12'59"W, 1720 m, 11 Feb 2016, F. Giraldo, A.

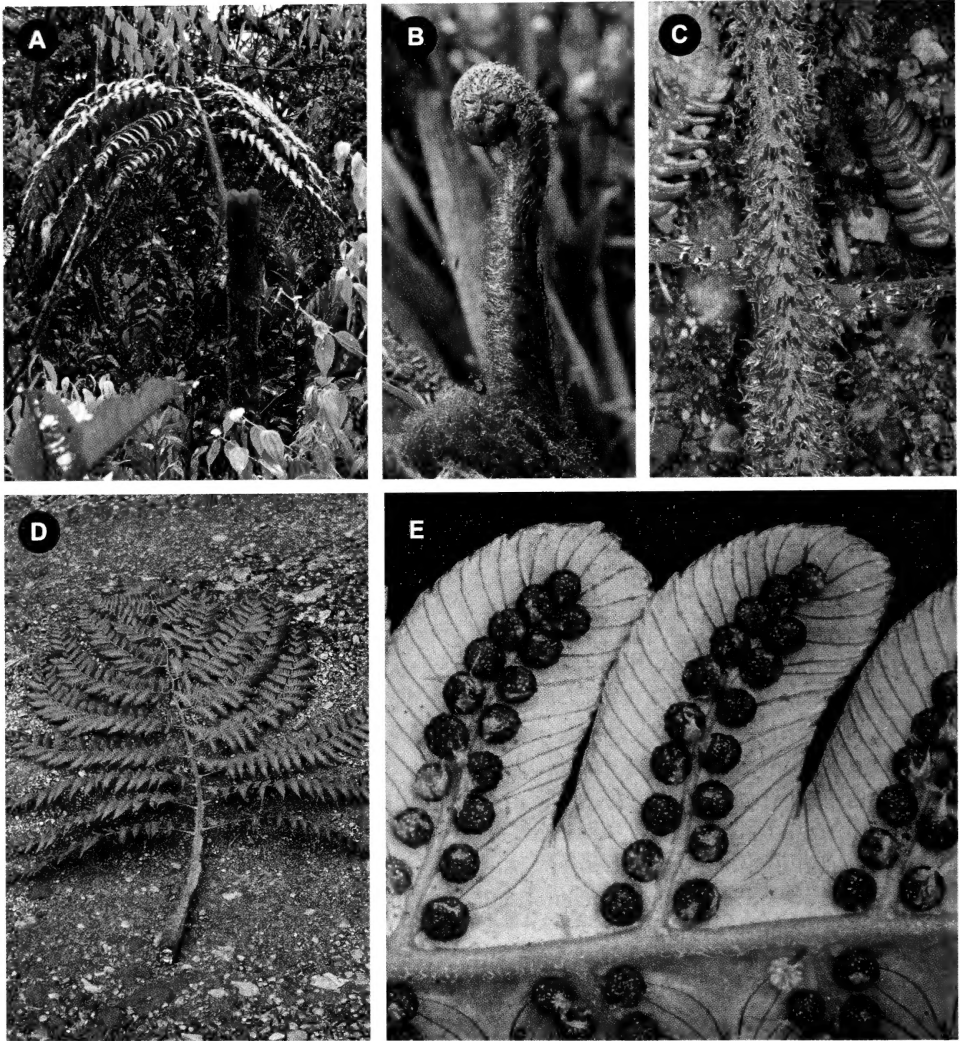


FIG. 2. *Cyathea callejasii* A. Habit, showing the exposed apex with colorful red scales, and the arching frond. B. Expanding crozier. C. Rachis of young frond abaxially, between lower pinnae, showing persisting scales and dense grayish scurf. D. Frond, adaxially; note the large patent basal pinnae. E. Segments, abaxially, with exindusiate sori, note the fine hairs on the costule (photos by F. Giraldo, corresponding specimen *Giraldo 3738A*, HUA).

*Salino, E. Dominguez & I. Moura 3738A* (holotype: HUA-202741/-202742/-202743!). **Fig. 2.**

Trunks to 3 m tall, 8–12 cm diam., without old petiole bases, densely covered with dark reddish brown scales with darker center, similar to petiole scales; apex not hidden between petiole bases, petioles inserted at a wide angle; trunk basally with adventitious buds, sprouting especially on decumbent trunks.

Fronds to 310 cm long, patent to arching, distally drooping. Petioles to 100 cm long, inermous or muricate with scattered prickles to 1 mm long, atropurpureous to blackish, matte, with dense scurf consisting of erect brown squamules to 1.0 mm long, some with dark brown teeth, with matted branched reddish brown hairs in basal half, grading into erect uniseriate hairs in distal half; petioles on each side with a discontinuous line of orange pneumathodes to  $4.0 \times 0.8$ –1.0 mm, scaly for most of its length, often up to lower pinnae. Petiole scales narrowly lanceate,  $10$ – $20 \times 2$ –3 mm, shiny, discordantly bicolorous brown with lighter brown to yellowish margins, bases darkened, weakly cordate, pseudopeltately attached, apices attenuate, undulate but not twisted; differentiated margins fragile, often abraded, the cell rows strongly exerted, in scales of distal petiole parts margins pale with dark brown teeth. Laminae to  $230 \times 120$  cm, ovate-elliptic, bipinnate-pinnatifid, firm chartaceous to subcoriaceous, matte, a rich dark green adaxially, paler abaxially; 10–12 pinna pairs, basal ones strongly reflexed, ca.  $1/2$  the length of the longest pinnae; apices gradually reduced. Frond axes (rachises, costae & costules) inermous, dark brown to atropurpureous abaxially and adaxially, matte to weakly shiny, adaxially pubescent with reddish brown, antrorsely curved multicellular hairs to 1 mm long, abaxially with similar but mostly shorter, more spreading hairs (0.5–1.0 mm), becoming paler towards the costules; costae to 3.0 mm, junctures of costae and rachises abaxially weakly swollen, each with only one large, conspicuous, weakly protruding elliptic aerophore to  $6.0 \times 2.5$  mm, pale brown, all junctures between the stronger axes with few linear-lanceate scales  $6$ – $12 \times 0.5$ –2.0 mm. Pinnae to 60 cm long,  $\pm$  patent, stalked to 3.5 cm, alternate, inarticulate, distally distinctly green-alate, distal segments not decurrently adnate before ending in a pinnatifid apical section. Pinnules to  $110 \times 28$  mm, stalked to 6 mm, inarticulate, 2–3 cm between the stalks, long-lanceate, bases truncate to weakly cordate, tips attenuate with crenulate margins; costules carneous to ochre or yellowish green on both sides, adaxially strongly prominent, ridged, densely hairy with tan to brown, antrorsely curved multicellular hairs to 1 mm long, abaxially weakly to strongly prominent, pubescent with pale brown hairs to 0.5 mm, also with flat, ovate-acuminate squamules to  $2 \times 0.5$ –1.0 mm, brown with paler, finely erose-denticulate margins with darker brown teeth; costules basally with one weakly raised pneumathode (to  $2 \times 1$  mm), light brown, inconspicuous. Segments to  $12 \times 5$ –6 mm, sessile, adnate, patent to ascending, falcate, tips rounded to obtuse, proximal segments  $\pm$  opposite,  $\pm$  equal to following segments, never remote from each other; sinuses acute, to 1.0 mm wide, sometimes occluded; margins crenulate, not differently incised in proximal segments of a pinnule; veins protruding adaxially and abaxially, midveins adaxially ridged, dark stramineous to yellowish brown, veins ending shortly before the margins, adaxially widened, deep orange-brown, glabrous on both sides, abaxially without squamules; sterile and fertile veins simple or forked. Sori 1.0–1.2 mm diam., costal to subcostal, parallel to the midvein, in the fork or on the back of veins; indusia lacking; receptacles globose, 0.3–0.4 mm

diam., some subtended by a small, ephemeral reddish brown scale, paraphyses few to absent, straight, reddish, much shorter than the sporangia (0.2 mm long). Spores ca. 45  $\mu$ m diam., pale brown *en masse*, tetrahedral-globose, exospore weakly verrucose, perispore baculate.

*Etymology*.—This species is dedicated to Colombian botanist Ricardo Callejas Posada (1954– ), University of Antioquia, Medellín.

*Distribution and Habitat*.—Northwestern Colombia (Chocó) in wet montane forests at 1720 m.

*Cyathea callejasii* appears intermediate between *C. hemiepiphytica* R.C.Moran and *C. nodulifera* R.C.Moran, having the trunk morphology of the former (*i.e.*, slender, without old petiole bases, fronds inserted at an almost right angle) and the lamina morphology of the latter (*i.e.*, outline more elliptic with persisting scales in axils of frond axes). A dense persistent pubescence of straight reddish brown multicellular hairs abaxially on the frond axes and the bicolorous petioles scales with pale brown to yellowish margins and darkened marginal teeth clearly separate *C. callejasii* from *C. hemiepiphytica* (hairs present but glabrescent, scales  $\pm$  concolorous) and *C. nodulifera* (only squamules and appressed branched hairs, scales weakly bicolorous but margins never as pale as in *C. callejasii*, without darker teeth). In its appearance, *C. nodulifera* is very distinct from the other two species, developing only a short stout trunk covered in prickly petiole bases from which long ascending and distally arching fronds emerge. In comparison, *C. callejasii* and *C. hemiepiphytica* have slender trunks with well-spaced fronds and without old petioles. In *C. hemiepiphytica*, the fronds are  $\pm$  patent with laminae weakly arching; in *C. callejasii*, the fronds are similarly attached to the trunk but the laminae are generally larger and thus distally more drooping than in *C. hemiepiphytica*.

The intermediate morphology could suggest a hybrid origin of *Cyathea callejasii*, and it indeed occurs where the geographical ranges of *C. hemiepiphytica* (Chocó-Esmeraldas region of northern Ecuador and southern Colombia) and *C. nodulifera* (Costa Rica/Panama to central Chocó region of Colombia) may overlap. The elevation range of *Cyathea callejasii* at 1720 m overlaps with that of *C. hemiepiphytica* (1200–1950 m) but not with that of *C. nodulifera* (up to 1380 m in Colombia, only to 1000 m in Panama). Moreover, *C. callejasii* occurred at the type locality without the two putative parents, albeit only in a small population, and the spores are regularly shaped and of even size. We thus regard it as a regularly sexually reproducing species.

3. *Cyathea cardenasii* Lehnert, F.Giraldo & W.Rodríguez, *sp. nov.* Type: COLOMBIA. Antioquia: San Luis, Quebrada “La Cristalina”, 07°14'08.4"N 75°02'05.7"W, 680 m, 2 Feb 2015, M. Lehnert 3028 with M. Kessler, W. Rodríguez, F. Giraldo (holotype: HUA-198559/-198570/-198571!; isotypes: BONN!, Z!). Fig. 3.

Trunks to 4 m tall, 6–8 cm diam., covered with old prickly petiole bases, sometimes petiole bases rotting off in older trunk parts; epidermis densely



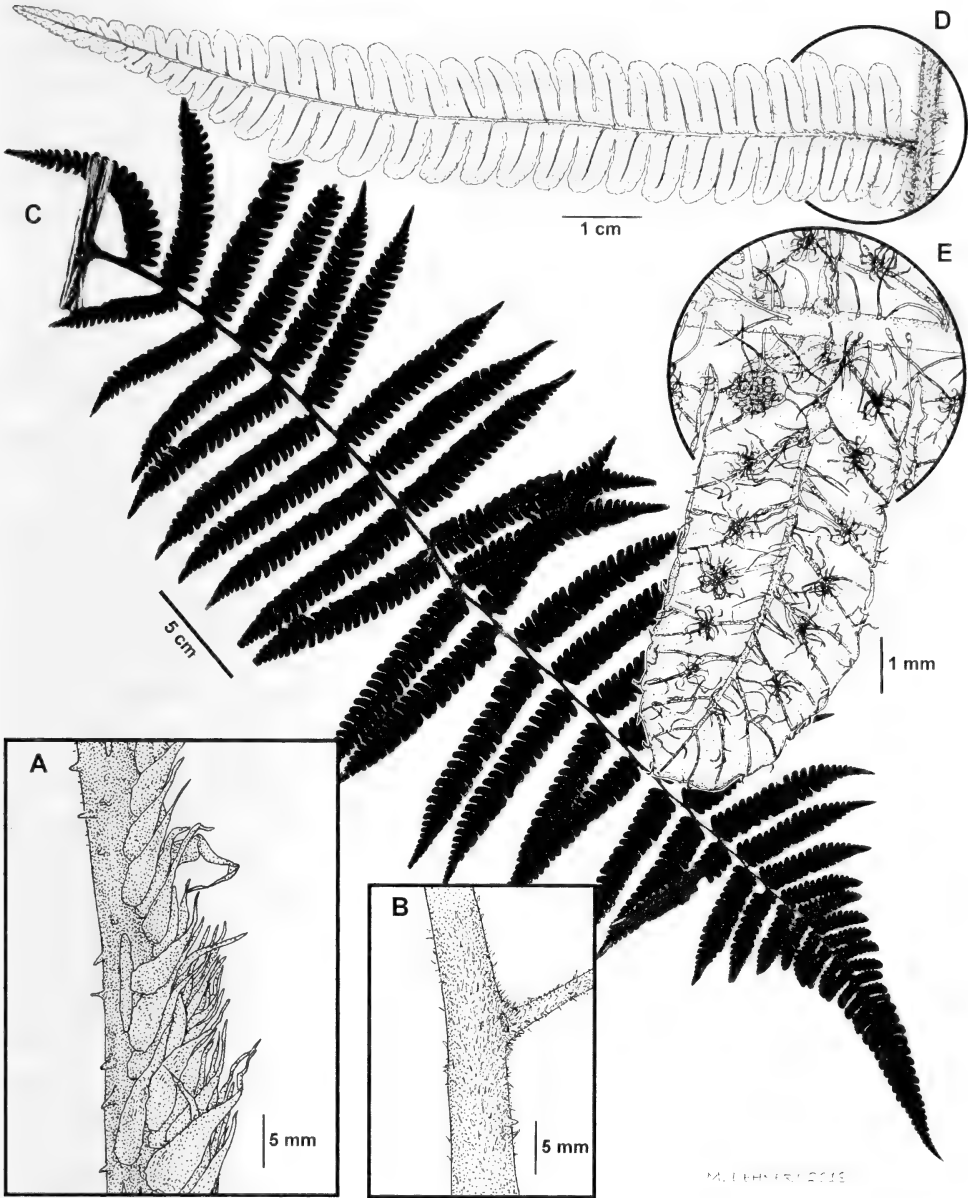


FIG. 3. *Cyathea cardenasii*. A. Petiole with scales. B. Junction of rachis and costa abaxially, showing inconspicuous elliptic aerophore and indument of short hairs. C. Pinna. D. Pinnule, adaxially. E. Segment abaxially, most sori shown without sporangia, showing the long, contorted paraphyses (A, B from Callejas et al. 4200, COL; C–E from Lehnert 3028, BONN).



covered with brown, narrowly lanceate scales, similar to petiole scales; apices hidden between petiole bases; without adventitious buds. Fronds to 290 cm long, erect to arching. Petioles to 95 cm long, basally aculeate with prickles to 4 mm long, dark brown to atropurpureous, rarely blackish, weakly shiny, with sparse to abundant, easily abraded scurf consisting of appressed reddish brown trichomidia and branched hairs, rarely with some larger lanceate squamules to ca.  $3.0 \times 1.5$  mm, orange-brown; with many multicellular hairs to 5 mm long; petioles on each side with a discontinuous line of lenticels to  $15 \times 1$  mm, orange-brown in dried material. Petiole scales long-lanceate,  $25\text{--}30 \times 3\text{--}6$  mm, rather thin-textured, bases cordate, basifixed to pseudopeltately attached, straight, apices long attenuate, strongly undulate and twisted; scales concolorous, auburn to orange-brown, differentiated margins persistent, the cell rows exserted, with short pale teeth. Laminae to  $195 \times 140\text{--}150$  cm, bipinnate-pinnatifid, firm-chartaceous, matte, dark-green adaxially, often blackish when dried, dark olive-green abaxially; apices gradually reduced. Frond axes (rachises, costae, costules) inermous, or rachises sparsely muricate in proximal parts, brown to dark purpureous abaxially and adaxially; pubescent with whitish to tan multicellular hairs to 2(–3) mm long, antrorsely curved adaxially, abaxially spreading, persistent, leaving the epidermis rough if abraded; costae 1.5–2.0 mm wide; junctures of costae and rachises not swollen, abaxially often black when dried, each with 1–2 inconspicuous, planar to weakly protruding, elliptic aerophores, to  $3.0 \times 1.5$  mm. Pinnae to 75 cm long, subsessile to stalked to 2.5 cm, 8–10 pairs per frond, patent to ascending, alternate, inarticulate, distally narrowly green-alate, with distal segments separately adnate before ending in a pinnatifid apical section; basal pinna pairs not much smaller than the medial pinnae, reflexed. Pinnules to  $130 \times 20$  mm, sessile to subsessile (stalked to 1 mm), inarticulate, 1.2–2.8 cm between the stalks/costules, lanceate to linear-oblong, truncate to cuneate basally, long-acute to attenuate apically with serrate to crenulate margins; costules dark carneous to atropurpureous adaxially and abaxially, proximally often darker; adaxially strongly prominent, ridged, and densely hairy with whitish to tan, spreading to appressed, multicellular hairs to 1.5 mm long, abaxially weakly to strongly prominent, densely and persistently scurfy like the costules, with many erect, white hairs to 2.0 mm long, also with few tan to brown, flat to subbullate squamules to 2 mm long, with flat to subulate apices; costules basally without visible pneumathodes, blackened in dried specimens. Largest segments  $9\text{--}12 \times 3\text{--}4$  mm, segments sessile, adnate, ascending, distally straight, tips obtuse, proximal segments alternate to subopposite, usually a bit shorter than the next segments, sometimes remote and then strongly crenate; sinuses acute to rectangular, to 1(–2) mm wide; margins crenulate to crenate; veins planar to weakly protruding adaxially and abaxially, dark carneous to atropurpureous or blackish, ending in the margins; veins adaxially and abaxially with many erect, white to yellowish white, multicellular hairs to 2 mm long on them, also along the margins and abaxially between the veins; midveins with few dark brown bullate squamules to  $2.0 \times 0.5$  mm; sterile veins simple or forked, fertile

veins forked. Sori 1.0(–1.2) mm diam., medial, in the fork of veins; indusia lacking; receptacles globose, 0.2–0.3 mm diam., paraphyses numerous, tortuous but not entangled, ends free, tan to reddish brown, longer than the sporangia (ca. 0.6 mm long) and persisting in over-mature sori. Spores not examined.

*Etymology*.—The epithet honors our friend and colleague Dairon Cárdenas López (1957– ), Instituto SINCHI, Bogotá.

*Distribution and Habitat*.—Northern Colombia (Prov. Antioquia), in the understory in evergreen premontane forest at 680–1300 m.

*Additional Specimens Examined (paratypes)*. COLOMBIA. Antioquia: Anorí, Refugio Bajo Cauca, Nechí, Finca El Cielo, Vereda Madre Seca, 6.4036111, -74.7605556, 780 m, *F. Giraldo 2534* (HUA, JAUM); Anorí, 7.2526000, -75.5176194, 800 m, *F. Giraldo 2543 A* (HUA, JAUM); Maceo, Vereda San Pedro, Finca San Pedro, 6.5825000, -75.0229167, 996 m, *O. Díaz 26* (HUA); Vereda San Pedro, Finca San Pedro, 6.9860111, -76.1190528, 970 m, Jun 2009, *P. Morales 337* (HUA); San Carlos, Corregimiento Alto Samaná, Vereda Miraflores, finca El Desespero, 6.0000000, -74.8333333, 750–890 m, *R. Callejas 8583* (HUA); Vereda La Rápida, escampadero Cantarrana, 1100 m, 18 Apr 2005, *J. Colorado 235* (HUA); San Luís, vía Medellín-Bogotá, Km 100–115, 7.1670000, -75.7336111, 1000–1300 m, 31 Mar 1987, *A.L. Arbelaéz 47* (HUA); 16 km SW de las partidas a San Luis, sobre la vía Medellín-Bogotá, Vereda La Josefina, 06°00'N, 74°50'W, 800 m, 26 Jun 1991, *R. Callejas et al. 4200* (COL); near Porcesito in valley of Río Medellín, 1100 m, 19 May 1946, *W.H. Hodge 6871* (COL, US); San Luis, Quebrada “La Cristalina”, 7.2356667, -75.0349083, 680 m, 2 Feb 2015, *M. Lehnert 3027 with M. Kessler, W. Rodríguez, F. Giraldo* (BONN, HUA, Z); San Rafael, Vereda. EL Charco, 1010–1200 m, 06°32'55"N, 75°08'19.3"W, Apr 1998, *J.A. Montes 353* (COL); Santo Domingo, Corregimiento Santiago, vertiente oriental de la Cordillera Central, 06°15'45"N, 75°01'55"W, 1789 m, 20 Jun 2014, *G. Restrepo 259* (HUA); Yolombó, Sector partidas Yolombó – Porce, 6.0833333, -74.8333333, 900–1200 m, *J. Colorado 378* (HUA).

*Cyathea cardenasii* differs from *C. lockwoodiana* (P.G.Windisch) Lellinger in having taller trunks to 4 m tall (vs. to 2.5 m tall in *C. lockwoodiana*), petiole scales 3–6 mm wide (vs. 1.5–3.0 mm wide), and paraphyses tortuous but not entangled ca. 0.6 mm long (vs. paraphyses heavily contorted and entangled, ca. 0.6–0.8 mm long). The paratypes *Callejas et al. 4200* and *Hodge 6871* were included under *C. lockwoodiana* in a previous treatment (Lehnert 2016).

*Cyathea cardenasii* differs from *C. margarita* Lehnert by sori more medial (vs. more marginal in *C. margarita*), hairs abaxially on axes and lamina to 2.0 mm long (vs. to 0.5 mm long), and petiole scales 25–30 × 3–6 mm (vs. 19 × 3.0–3.5 mm) concolorous orange-brown (vs. dark brown to castaneous with narrow, paler brown to whitish margins).

4. ***Cyathea catenata*** Lehnert, F.Giraldo & W.Rodríguez, *sp. nov.* Type: COLOMBIA. Valle de Cauca: Old road Dagua-San Buenaventura, 03°37.174'N, 76°55.744'W, 550 m, 09 Feb 2015, *M. Lehnert 3095 with F.*

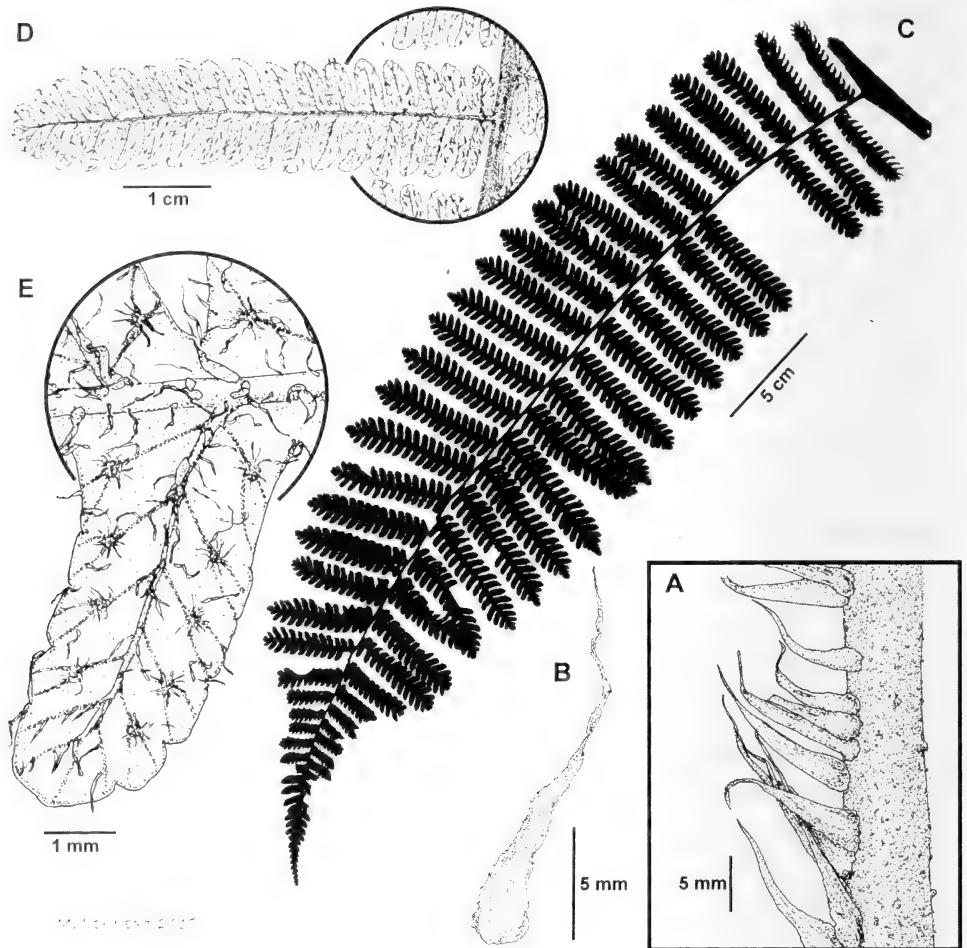


FIG. 4. *Cyathea catenata*. A. Petiole with scales. B. Lager petiole scale. C- Pinna. D. Pinnule, adaxially. E. Segment abaxially, sori shown without sporangia, showing the relatively short paraphyses (from Lehnert 3095, BONN).

*Giraldo & W. Rodriguez* (holotype: HUA-202566/-202567/-202568!, isotype: BONN!). **Fig. 4.**

Trunks to 2 m tall, slender, 4–5 cm diam., not prickly, without old petiole bases; apices hidden by fascicles of petioles; without adventitious buds. Fronds to 200 cm long, patent to weakly arching from ascending petioles, larger fronds distally weakly drooping. Petioles to 60 cm long, inermous to weakly muricate, with widely spaced blunt prickles less than 1 mm long, epidermis dark stramineous to reddish brown, usually basally slightly darker, weakly shiny, scurf absent or very scarce near petiole base, consisting of appressed, tan to brown branched hairs and highly dissected squamules to 0.6 mm long; petioles scaly only in lower third, scales not reaching up to the

rachises. Petiole scales lanceate to linear-lanceate, to  $15.0 \times 2.0$ – $3.5$  mm, bases cordate or round, pseudopeltately to peltately attached, apices attenuate, straight or weakly falcate, flat; concordantly bicolorous to nearly concolorous, dark brown (atropurpureous to castaneous in backlight) with brown to yellowish margins; differentiated margins narrow, without setae, erose-dentate, fragile, often partially abraded. Laminae to  $160 \times 90$  cm, broad-elliptic, bipinnate-pinnatifid, firm-herbaceous, dark green adaxially, pale gray-green abaxially; apex gradually reduced or a broad subconform section. Rachises inermous, weakly shiny, dark brown to purpureous abaxially and adaxially, rarely dark stramineous to ochre; adaxially densely hairy with white to tan, antrorsely curved multicellular hairs  $1.0$ – $1.5$  mm long, abaxially and on the sides with thick spreading white to tan hairs ( $1.0$ –) $1.5$ – $2.0$  mm long, catenate in dried specimens, and with few small brown lanceate scales (to  $1.0 \times 0.5$  mm), without scurf. Pinnae to 45 cm long, sessile to subsessile (appearing short-stalked to 1 cm when basal pinnules are missing), ca. 16 pairs per frond, weakly ascending, alternate, inarticulate, distally distinctly green-alate, distal segments weakly decurrently adnate before ending in a pinnatifid apical section; basal pinna pairs ca.  $2/3$  the length of the medial pinnae, weakly reflexed. Costae to 1.5 mm wide, inermous or sparsely verrucate, dark brown to ochre abaxially, greenish to dark brown adaxially; with the same indument as on the rachises; junctures of costae and rachises often with dense scurf and some bullate squamules; junctures weakly swollen abaxially, each bearing a planar elliptic pneumathode to  $2 \times 1$  mm, pale brown, with an adjacent conspicuous black spot in dried specimens (foliar nectary). Largest pinnules  $52$ – $78 \times 11$ – $17$  mm, pinnules sessile, inarticulate, ca. 1.5 cm between the stalks/costules, linear-oblong to oblanceolate, bases cuneate to rounded, often inequilateral, apices round to obtuse, rarely broadly acuminate with crenate margins; costules dark carneous to blackish green adaxially and abaxially, strongly prominent and densely hairy adaxially with white, curved multicellular hairs to 1.5 mm long; abaxially planar or weakly prominent, with many erect, white, uniseriate multicellular hairs  $1.0$ – $1.5$ –( $2.0$ ) mm long, some also between the veins, and few to many bullate pale to dark brown squamules to  $1.0 \times 0.5$  mm, with entire margins and attenuate tips; costules basally without visible pneumathodes but with blackened area in dried specimens. Largest segments  $7.0$ – $8.0 \times (2.0)$ – $2.5$ – $3.0$  mm, segments ascending, straight to distally falcate, tips obtuse to rounded, sinuses acute to obtuse,  $1.0$ – $2.0$  mm wide; proximal segments alternate to subopposite,  $\pm$  the same size as following segments, never remote from each other; margins shallowly to strongly crenate, not differently incised in proximal segments of a pinnule; veins planar on both sides or weakly protruding adaxially, brown to blackish, equally hairy on both sides with uniseriate multicellular, white to tan hairs  $1.0$ – $1.5$  mm long, partially to wholly catenate in dried specimens, the same hairs abaxially also between the veins; midveins abaxially with few to many bullate brown squamules  $1.0 \times 0.5$  mm, with entire margins and elongate tips; sterile veins simple or forked, fertile veins mostly forked. Sori 1.0 mm diam., medial to supramedial, parallel to the margins, in fork of veins; indusia

lacking; receptacles globose, 0.2–0.3 mm diam., not subtended by squamules, paraphyses numerous, pale brown to reddish brown, same length as sporangia (0.3–0.4 mm long). Spores not examined

*Etymology*.—The epithet refers to the white catenate hairs evident on the laminae of dried specimens.

*Distribution and Habitat*.—Only known from the southern Chocó region in Colombia (Depts. Valle de Cauca, Nariño) in ever-wet forests at 300–1000 m.

*Additional Specimens Examined (Paratypes)*. COLOMBIA. Nariño: Nariño-Junin, 5 km en dirección a Barbacoas, 1000 m, 20 Dec 1972, W. Hagemann & N. Leist 1731 (COL). Valle del Cauca: Buenaventura Municipio Bajo Anchicayá, 03°45'N, 76°50'W, 300 m, 19 Oct 1989, A. Gentry & O. Rangel 68310 (COL, MO); *ibid.*, A. Gentry & O. Rangel 68282 (COL, MO), *ibid.*, A. Gentry & O. Rangel 68531 (COL, MO); *ibid.*, 20 Oct 1989, A. Gentry & O. Rangel 68597A (COL, MO), *ibid.*, 21 Oct 1989, A. Gentry & O. Rangel 68634A (COL, MO).

*Cyathea catenata* belongs to the group of *Cyathea tortuosa* R.C.Moran (Lehnert *et al.*, unpublished data), a group of slender-trunked understory species with shiny green laminae. It differs from other species in the group by hairs on both sides of the veins abundant, usually catenate, thick, whitish, and spreading. The other species in the group (*i.e.*, *C. darienensis* R.C.Moran, *C. tortuosa*, *C. schiedeana* (C.Presl) Domin, *C. wendlandii* (Kuhn) Domin) have hairs only sparsely present on the veins adaxially, and the hairs are usually not notably catenate, either because they are thick and turgid or much thinner and twisted in dried specimens. *Cyathea catenata* is very similar in appearance to *Cyathea tortuosa* R.C.Moran, with slender trunks 4–5 cm diam., concolorous appearing dark brown petiole scales and blunt-tipped pinnules. *Cyathea catenata* stands apart by its shallowly to strongly crenate segment margins (*vs.*  $\pm$  subentire in *C. tortuosa*) and the thicker, spreading hairs on the segments (*vs.* most hairs on segments tortuous, appressed in *C. tortuosa*), which are usually catenate in dried specimens. *Cyathea darienensis* differs in the same characters from *C. catenata* (*i.e.*, segments entire, less hairy, spreading hairs on segments not thick) and has more and larger dark brown bullate squamules on costules.

With its narrow crenate segments, *Cyathea catenata* resembles *C. lasiosora* (Kuhn) Domin of the Amazon basin but can be distinguished by persistent catenate hairs (*vs.* often glabrescent, with hairs turgid to collapsed but not catenate in *C. lasiosora*) and paraphyses not surpassing sporangia (*vs.* surpassing closed sporangia). Specimens of *C. catenata* may also be the basis for some erroneous records of *C. pilosissima* (Hook.) Domin, a species currently known only from the eastern Andean slopes of Peru, from the Chocó region (Lellinger, 1989). *Cyathea pilosissima* is distinguished by the spreading red hairs on the frond axes, the densely hairy petiole and the whitish petiole scale margins, which are characters absent in *C. catenata*.

Another similar species, herein described as *C. kessleriana*, differs from *C. catenata* by being larger, having more hairs on the laminae, and lacking scurf on the petioles. *Cyathea catenata* differs further in being equally hairy on both sides with uniseriate multicellular (*vs.* veins hairier abaxially than adaxially in

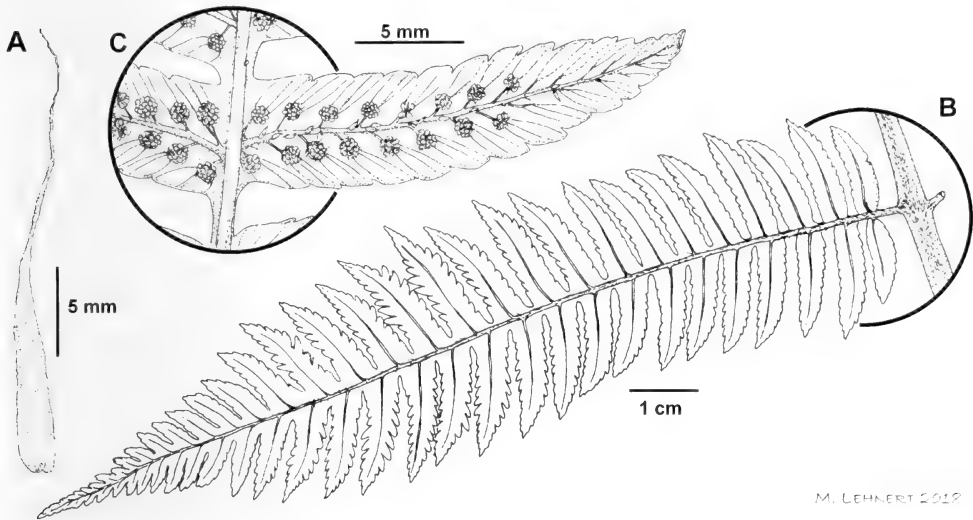


FIG. 5. *Cyathea coloradoana* A. Petiole scale. B. Pinnule, adaxially. C. Segment, fertile, abaxially (from Colorado 651, HUA).

*C. kessleriana*) and having slightly smaller segments with wider sinuses (segments to  $8 \times (2.0-2.5-3.0)$  mm, sinuses 1.0–2.0 mm wide in *C. catenata* vs. to  $11 \times 3-4$  mm, sinuses 0.5–1.0(–2.0) mm wide in *C. kessleriana*) and more strongly crenate margins.

*Cyathea margarita* is another relatively small exindusiate species from the Chocó-Esmeraldas region that may be found together with *C. catenata* and *C. kessleriana*, which can be easily distinguished by its pale brown to yellowish axes (vs. dark brown to atropurpureous in *C. catenata* and *C. kessleriana*), abundant short acicular hairs between the veins abaxially (vs. hairs absent or long and catenate), and sori notably positioned close to the margins (vs.  $\pm$  sori medial).

**5. *Cyathea coloradoana*** Lehnert, F.Giraldo & W.Rodriguez, *sp. nov.* Type: COLOMBIA. Antioquia: Municipio Anorí, Vereda Providencia, sector cerca al Puente de la Quebrada Providencia,  $07^{\circ}20'54''\text{N}$ ,  $75^{\circ}01'15''\text{W}$ , 200 m, 14 Jun 2011, *J. Colorado & W. Uribe 651* (holotype: HUA-178335/-178336/-178337!). **Fig. 5.**

Trunks to 4 m tall, to 12 cm diam., otherwise unknown. Fronds to ca. 200 cm long. Petioles to 70 cm long, sparsely muricate to short-aculeate, dark brown, basally becoming darker, shiny, without scurf except for sparse appressed, tan to brown trichomidia near the base; basally with a discontinuous line of elliptic pneumathodes to  $8 \times 1.5-2.0$  mm, dark brown in dried material; petiole scales restricted to proximal half of petioles. Petiole scales lanceate to linear-lanceate,  $25 \times 2$  mm, bases weakly cordate, basifixed to pseudopeltately attached, apices elongate, twisted; concolorous dark brown to castaneous;

differentiated margins persistent, very narrow, reduced to a line of teeth in distal parts. Laminae to ca.  $130 \times 170$  cm, bipinnate-pinnatifid to partially tripinnate, broadly ovate, herbaceous, dark green adaxially, pale gray-green abaxially; apices  $\pm$  abruptly reduced to subconform pinnate-pinnatifid sections. Rachises inermous, weakly shiny, dark brown abaxially and adaxially, without scales; in distal parts with antrorsely curved, white to tan multicellular hairs 0.5–0.8 mm long adaxially, abaxially glabrous, epidermis smooth. Largest pinnae to 90 cm long, stalked to 3 cm, pinnae patent to ascending, alternate, inarticulate, 7 pairs per frond, distally weakly green-alate, distal segments adnate before ending in a pinnatifid apical section; basal pinna pairs reflexed, stalked to 5 cm, ca.  $1/2$  the size of the medial pinnae, with the proximal basiscopic pinnules reduced or missing. Costae to 3 mm wide, inermous, dark brown abaxially and adaxially, adaxially with antrorsely curved, uniseriate hairs (0.8–1.0 mm long), abaxially glabrous or with remnants of reddish brown scurf of appressed branched hairs; junctures not swollen, each bearing abaxially a dark brown planar, elliptic pneumathode to  $3.0 \times 1.5$  mm, with a conspicuous black spot below (foliar nectary). Largest pinnules  $135\text{--}152 \times 38\text{--}45$  mm, subsessile to stalked to 5 mm, 2.9–3.3 cm between stalks/costules, pinnules inarticulate, linear-oblong to lanceate, bases round to cuneate, apices long-acuminate to attenuate, with crenulate to serrulate margins; costules carneous to orange-brown adaxially and abaxially, adaxially strongly prominent, ridged, with many whitish to tan, antrorsely curved multicellular hairs to 0.5(–1.0) mm long; abaxially weakly to strongly prominent, glabrous or glabrescent with remnants of scurf, with few to many dark brown to castaneous scales to  $1.0 \times 0.5$  mm, a mixture of larger flat lanceate ones with entire margins, bullate ones with filiform tip, and smaller flat lanceate scales with fimbriate margins; costules basally without visible pneumathodes, but often with a black spot abaxially in dried specimens. Largest segments  $18\text{--}22 \times 5.0\text{--}7.5$  mm, segments elongate to long-deltate, patent to ascending, straight to distally weakly falcate, tips acute; proximal segments alternate to subopposite, notably smaller than following segments, sometimes remote from each other, then connected by a thin strand of green tissue; sinuses acute to rectangular, 1.5–2.0(–3.0) mm wide; margins serrulate, deeply so towards the tips of distal segments, in proximal segments of a pinnule identically incised; midveins strongly protruding, adaxially ridged, lateral veins planar on both sides or weakly protruding adaxially, green or brown, adaxially with few hairs on the midveins, abaxially without uniseriate hairs but with remnants of scurf (reddish brown branched hairs) and some bullate and flat squamules like on the costules; sterile veins simple or forked, fertile veins forked. Sori 0.8–1.0 mm diam., each with ca. 40 sporangia, medial to inframedial, parallel to margins, usually in fork of veins; indusia lacking; receptacles globose, ca. 0.2 mm diam., paraphyses many, reddish or pale brown, catenate, tortuous, slightly longer than the sporangia (0.5 mm long). Spores not examined.

*Etymology*.—Named after Jhon Jairo Colorado (1965– ), Colombian botanist and plant illustrator, collector of the type specimen.



*Distribution and Habitat.*—Known only from the type specimen, found in northern Colombia (Dept. Antioquia) in lowland rain forests at 200 m.

*Cyathea coloradoana* resembles *C. myosuroides* (Liebm.) Domin in scale color and structure (*i.e.*, the differentiated scale margin reduced to a row of marginal teeth at least near the scale tip), laminar indument (*i.e.*, veins abaxially densely hairy with spreading to antrorsely curved, white, multicellular hairs 0.5–0.8(–1.0) mm long, also with few to many dark brown to castaneous, flat, lanceate scales to  $2 \times 1$  mm) and sori (*i.e.* exindusiate with long paraphyses). *Cyathea coloradoana* differs in having fewer pinnae (ca. 7 pairs per frond in *C. coloradoana* vs. 10–11 pairs in *C. myosuroides*) and larger pinnules ( $135\text{--}152 \times 38\text{--}45$  mm vs.  $85\text{--}115\text{--}(140) \times 18\text{--}20\text{--}(25)$  mm in *C. myosuroides*) with longer, conspicuously deeply serrate tips and softer laminar texture, and lacking long, multicellular, marginal cilia in the scales of the laminar indument. Regarding the laminar texture and the serrate segment margins, *C. coloradoana* resembles more *C. microdonta*. Again, *C. coloradoana* is larger in most parts of the frond (largest pinnules  $135\text{--}152 \times 38\text{--}45$  mm in *C. coloradoana* vs.  $55\text{--}115 \times 9\text{--}22$  mm in *C. microdonta*) but has narrower petiole scales ( $25 \times 2$  mm vs.  $14\text{--}32 \times 2.5\text{--}4.5$  mm).

The slightly oblanceolate segments of *Cyathea coloradoana* with their distally more deeply incised margins are very conspicuous. We suspect that this is usually a sign of hybrid origin, as this rare feature is mainly known from the documented hybrids *C. × hombersleyi* (Maxon) Stolze, *C. × wilsonii* (Hook.) Domin, and further genetically confirmed hybrids that still wait formal recognition (Lehnert *et al.*, unpubl. data). We want to point out that this aspect needs further investigation but at the same time that we do not have any further evidence for a hybrid origin of *C. coloradoana*.

6. *Cyathea kessleriana* Lehnert, F.Giraldo & A.Tejedor, **sp. nov.** Type: COLOMBIA. Risaralda: Municipio Santa Cecilia, via que conduce desde Pueblo Rico a Santa Cecilia, al borde de la via principal,  $05^{\circ}19'45.0''\text{N}$ ,  $76^{\circ}10'23.72''\text{W}$ , 300–700 m, *F. Giraldo & A. Tejedor 3130* (holotype: HUA-201975/-201976/-201977!). **Fig. 6.**

Trunks to 3 m tall, erect, to 5 cm diam., without old petiole bases, no skirt of dead fronds; without adventitious buds. Fronds to 210 cm long,  $\pm$  patent to weakly arching. Petioles 27–45 cm long, sparsely aculeate with few prickles to 1 mm long, brown to dark brown, matte to weakly shiny, with easily abraded scurf consisting of appressed, light brown squamules, largely missing in older fronds; petioles basally with few light to orange-brown pneumathodes to  $15 \times 1.5$  mm on each side, only scaly near petiole base. Petiole scales narrowly lanceate,  $12\text{--}16 \times 2.0\text{--}3.5$  mm, shiny, concolorous dark brown or with lighter brown margins, bases cordate, pseudopeltately attached, apices long acute, straight to falcate, undulate or weakly twisted; differentiated margins narrow (ca. 0.2 mm wide), fragile, often abraded, the cell rows strongly exerted. Laminae to  $165 \times 110\text{--}120$  cm, ovate, bipinnate-pinnatifid, firm herbaceous, matte, rich green adaxially, often blackish when dried, grayish green abaxially;

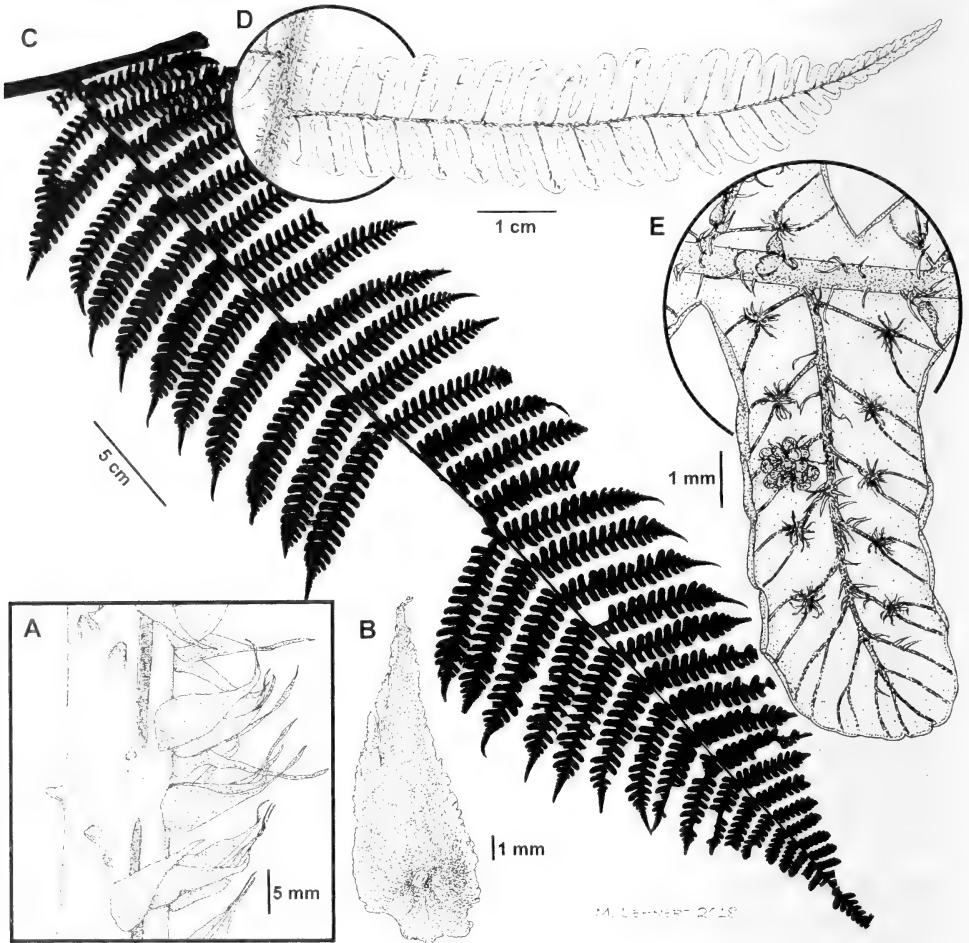


FIG. 6. *Cyathea kessleriana*. A. Petiole with scales, showing two pneumathodes. B. Petiole scale, showing point of peltate attachment. C. Pinna. D. Pinnule, adaxially. E. Segment abaxially, most sori shown without sporangia, showing the straight paraphyses (from *Giraldo 3130*, BONN).

apices abruptly reduced to broad subconform sections. Rachises inermous or proximally muricate, brown to dark brown abaxially and adaxially; adaxially with pale reddish brown, multicellular, antrorsely curved hairs 1.0–2.0 mm long, abaxially with similar persistent hairs but paler and spreading, their indurated bases leaving the cortex scabrous. Largest pinnae 55–60 cm long, pinnae patent to weakly ascending, mostly sessile, ca. 9 pairs per frond, alternate, inarticulate, distally narrowly green-alate, distal segments adnate before ending in a pinnatifid apical section; basal pinnae 1/2 the length of longest pinnae, stalked to 1 cm, patent to weakly reflexed. Costae to 3 mm wide, inermous, abaxially dark stramineous to yellowish brown, adaxially darker, adaxially with antrorsely curved to appressed, whitish to pale brown

uniseriate hairs 1.0–1.5 mm long, abaxially with many spreading white multicellular white hairs to 1.5(–2.0) mm long and few scattered brown to dark brown bullate squamules to  $1.0 \times 0.5$  mm, with acuminate tips; junctures of costae and rachises abaxially weakly swollen, each with an inconspicuous, planar to weakly protruding elliptic pneumathode to  $3.0 \times 1.5$  mm, with a dark brown to blackish spot below (foliar nectary). Largest pinnules  $61\text{--}97 \times 11\text{--}18$  mm, pinnules sessile, inarticulate, ca. 1.5–2.0(–2.5) cm between the costules, linear-oblong to oblanceate, bases truncate to cuneate, tips obtuse to broadly acute, in large plants also short-attenuate, with subentire to crenate margins, costules carneous to greenish brown on both sides, adaxially strongly prominent, ridged, abaxially weakly to strongly prominent, adaxially densely hairy with whitish to pale brown, curved to appressed, uniseriate hairs 1.0–1.5 mm long, abaxially with many stout white hairs 1.0–1.5 mm long and some scattered, weakly bullate, ovate-acuminate, dark brown squamules  $1.0 \times 0.5$  mm, with entire margins and subulate to elongate tips; costules basally with small inconspicuous pneumathodes to  $1.0 \times 0.5$  mm, area mostly black in dried specimens. Largest segments  $7\text{--}11 \times 3\text{--}4$  mm, sessile, adnate, patent to weakly ascending, distally straight to weakly falcate, tips obtuse to rounded, proximal segments alternate to subopposite,  $\pm$  the same size as following segments, never remote; sinuses acute to obtuse, 0.5–1.0(–2.0) mm wide; margins subentire to weakly crenate, near the tips also dentate or rarely deeply crenate, proximal segments with margins incised  $\pm$  symmetrically; veins planar adaxially and abaxially, greenish to blackish, ending in the margins; veins hairier abaxially than adaxially, with erect, tan to white uniseriate hairs (0.5–)1.0–1.5 mm long, thick, often catenate in dried specimens, adaxially hairs sparse on midveins, rare on lateral veins, abaxially numerous on midveins, thick, often catenate in dried specimens, fewer and thinner on lateral veins, also sparsely between the veins, here also sometimes with brown dots (unicellular trichomidia and bases of lost hairs); abaxially with few brown to dark brown, weakly to strongly bullate squamules to  $1.0 \times 0.5$  mm; sterile veins simple or forked, fertile veins mostly forked. Sori 0.6–0.8 mm diam., medial to inframedial, parallel to the margins, in the fork of veins, mature dark orange-brown; indusia lacking; receptacles globose, 0.2–0.3 mm diam., not subtended by a scale, paraphyses numerous, straight, pale brown to reddish, of the same length as or shorter than the sporangia (0.3–0.4 mm long). Spores tetrathedral-globose, pale yellow, perispore not examined.

*Etymology*.—The epithet honors our friend and mentor, Michael Kessler (1967– ), University of Zurich, Switzerland.

*Distribution and Habitat*.—Western Colombia (Depts. Chocó, Valle de Cauca) in wet montane forests at 300–1350 m.

*Additional Specimens Examined (Paratypes)*. COLOMBIA. Chocó: Carmen de Atrato, al lado de la vía Ciudad Bolívar-Quibdó,  $05^{\circ}46'17.1\text{N}$ ,  $76^{\circ}14'24.5\text{W}$ , 1300 m, 12 Feb 2016, *F. Giraldo* 3753 (HUA); San José del Palmar, Vereda La Badea, 920 m, 24 Jan 1983, *P. Franco* 1835 (COL); *Ibid.*, Vereda Portachuelo, Fca. Barro Blanco, 1300 m, 15 Jan 1983, *Santiago Diaz* 3602 (COL); *Ibid.*, Vereda Portachuelo, Hacienda Barro Blanco, 1350 m 15 Jan 1983, *P. Franco*

1319 (COL); Nóvita, Vereda Curundó, margen izquierda del río Ingará, 550 m, 01 Dec 1983, *P. Franco 1100* (COL). Valle de Cauca: Buenaventura, Municipio Bajo Anchicayá, Levantamiento, 03°45'N, 76°50'W, 300 m, *A. Gentry, O. Rangel & curso Postgrado-Botánico 68531* (COL, MO).

*Cyathea kessleriana* is best described as a hairy version of *C. darienensis* with fewer bullate squamules. In direct comparison, *C. kessleriana* has segment margins notably more crenate than *C. darienensis*, veins with longer, thicker, and paler hairs (1.0–1.5 m long, whitish catenate in *C. kessleriana* vs. 0.5(–1.0) mm long, tan to brown in *C. darienensis*) and only some scattered weakly bullate dark brown squamules  $1.0 \times 0.5$  mm (vs. squamules strongly bullate, frequent to abundant).

From *Cyathea catenata*, *C. kessleriana* differs in having fewer pinnae on average (ca. 9 pinna pairs per frond in *C. kessleriana* vs. to 16 pairs in *C. catenata*), being abaxially hairier than adaxially on the veins (vs. equally hairy on both sides), and having slightly larger segments with narrower sinuses (segments  $7\text{--}12 \times 3\text{--}4$  mm, sinuses 0.5–1.0(–2.0) mm wide in *C. kessleriana* vs. segments to  $8 \times (2.0\text{--})2.5\text{--}3.0$  mm, sinuses 1.0–2.0 mm wide in *C. catenata*).

*Cyathea kessleriana*, like *C. catenata*, stands out within the *C. tortuosa* alliance by having scabrous axes due to the persisting strong hairs. The other species of this alliance (including *C. darienensis*, *C. tortuosa*, *C. schiedeana* and *C. wendlandii*) are either glabrous or have sparse, finer hairs that are not detectable by touch.

**7. *Cyathea pacis*** F.Giraldo, W.Rodríguez & A.Tejedor, *sp. nov.* Type: COLOMBIA. Antioquia: Mpio. Ituango, Vereda San Pablo del Río Sucio, Finca Guasimal, Parque Nacional Natural Paramillo, cerca al Alto del Oso, quebrada Santa Bárbara, (ca. 07°20'51.14"N, 75°52'08.11"W) 1750–1810 m, 15 May 2003, *F. Giraldo, W. Rodríguez & J. Colorado 2622* (holotype: HUA-202137/-202138/-202139!). **Fig. 7.**

Trunks to 2.5 m, straight, massive, 12 cm diam., with old petioles; densely covered with concolorous pale brown to stramineous scales like those on the petioles; apices hidden between petiole bases; without adventitious buds. Fronds to 310 cm long, arching on erect petioles, clustered at trunk apex, unfurling only one at a time. Petioles to 100 cm long, aculeate with prickles to 7 mm long, scattered and hidden between dense petiole scales; epidermis brown, matte, with scattered scurf of white lacerate flat lanceate squamules 1–2 mm long; hairs absent. Petiole scales thin-textured, lustrous, linear-lanceate, bases cordate, pseudopeltately to peltately attached, apices long tapering, twisted, larger scales to  $50 \times 2.5\text{--}3.5$  mm, concolorous pale brown to weakly bicolorous with paler to white margins, smaller ones to  $20 \times 1.5\text{--}2.0$  mm, mostly concolorous stramineous or with an apical brown central stripe, differentiated margins reduced to few or a single cell row, cell rows not exerted, entire or with few distant unicellular teeth; scales covering petiole densely and persistently, reaching up to most parts of the rachis. Laminae to  $210 \times 120$  cm, ovate-elliptic, bipinnate with gradually reduced, inarticulate

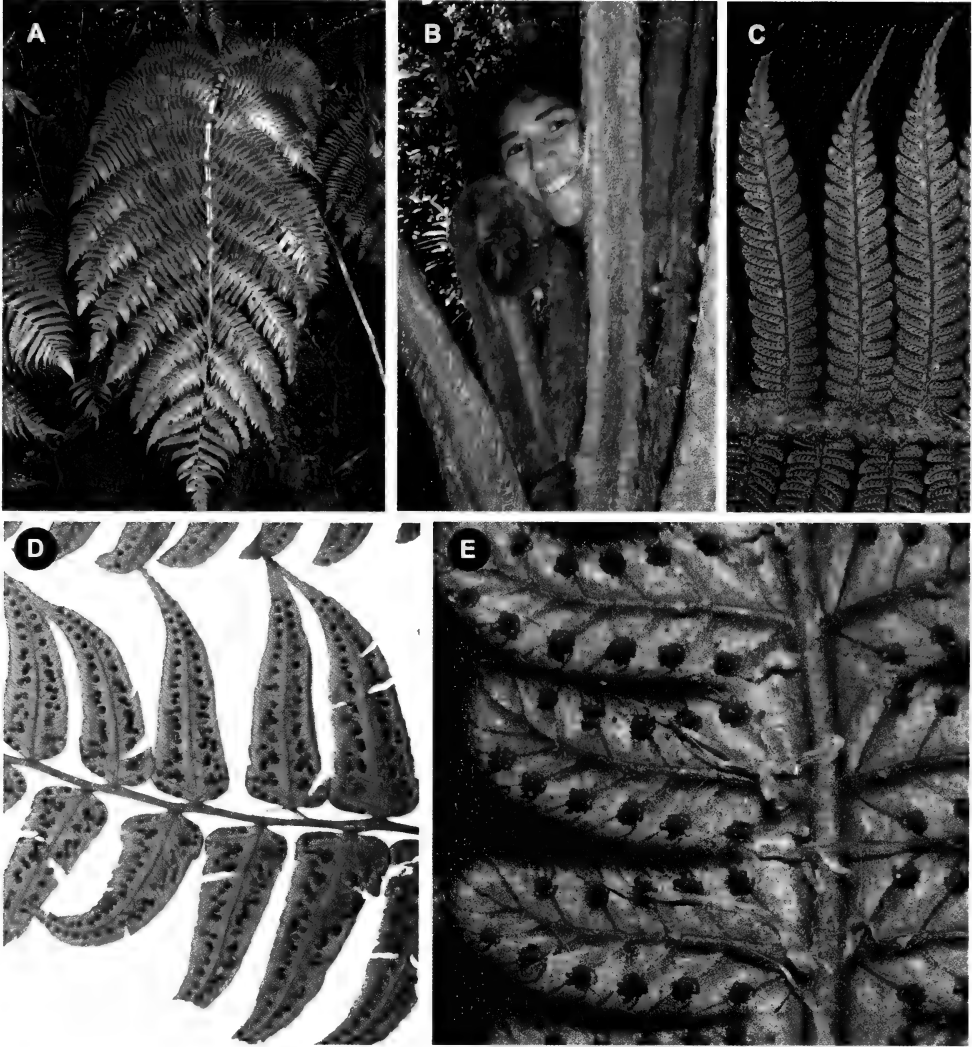


FIG. 7. *Cyathea pacis*. A. Habit, showing arching-drooping fronds. B. Apex with expanding crozier; with Gloria Calatayud. C. Larger pinnules abaxially, showing the persisting pale scales on the costa. D. Distal part of pinna abaxially, with entire pinnules (Giraldo 2622, HUA). E. Segments abaxially, with overmature sori, most sporangia missing; note the ascending hemitelioid indusia, best visible on the right side (photos by A. Tejedor).

apices in mature plants, subcoriaceous, adaxially shiny dark green (blackish when dried), abaxially matte olive-green. Rachises basally sparsely aculeate with scattered prickles to 0.4 mm long, brown to dark brown, adaxially often blackish and with few appressed trichomidia, multicellular hairs absent, on the sides and abaxially covered with lanceate scales similar to petiole scales, concolorous white to stramineous, some with brown basal spot and apical stripe, to  $15 \times 2$  mm; rachises distally not green alate. Pinnae to 65 cm long,

alternate, patent to distally weakly ascending, inarticulate; only distally green-alate before ending in a pinnatifid apical section, distal segments free to adnate, not basally decurrent; basal pinnae ca.  $1/3$  the length of longest pinnae, reflexed. Costae to 3 mm wide, inermous, brown to dark brown, adaxially darker than abaxially; adaxially with appressed reddish brown multicellular hairs to 1 mm long, rather sparse, abaxially without hairs, basally with scaly indument like on the rachises; junctures of costae and rachises not or weakly swollen, each abaxially with a dark pneumathode  $2-3 \times 1-2$  mm. Largest pinnules  $155 \times 22-25$  mm, subsessile with stalks to  $1(-2)$  mm, linear-lanceate, lobed  $1/5$  to  $3/4$  towards the costules, smaller ones sessile, lanceate with coarsely crenate to subentire margins,  $2.0-2.6$  cm between the stalks/costules, pinnules basally mostly truncate (larger ones weakly cordate, smaller ones weakly cuneate to rounded), basal lobes not covering the costae; apices attenuate to caudate with serrate margins; costules blackish brown to dark carneous, adaxially ridged and with few hairs ( $0.5-1.0$  mm long), prominent and glabrous abaxially, basally without visible pneumathode, with a dark spot; lobes round to obtuse and weakly falcate, margins entire, weakly sinuous to widely and shallowly dentate; most veins differentiated into a prominent brown midvein and planar to weakly raised lateral veins, the basal ones arising from the midvein, connivent to sinuses or ending blindly below then, joined between the lobes by an anastomosing vein, few lateral veins also forming anastomoses; veins adaxially glabrous, abaxially lacking hairs but with appressed brown unicellular trichomidia, also between veins; sterile and fertile veins simple or forked. Sori  $1.0-1.2$  mm diam., medial to inframedial,  $\pm$  equidistant between midveins and margins in lower half of segment, slightly closer to midvein in upper half of segment, on the back of veins; indusia hemitelioid, brown, reaching  $1/3-1/2$  around the receptacles, arching, often split in two lobes at maturity; receptacles globose,  $0.3-0.4$  mm diam., paraphyses few, fragile, mostly absent, reddish brown, straight, shorter than the sporangia ( $0.2-0.3$  mm). Spores not examined.

*Etymology*.—The specific epithet “of peace” reflects the hope of permanent peace in Colombia.

*Distribution and Habitat*.—Northern Colombia (Dept. Antioquia), in wet montane forests at 1750–1810 m.

*Cyathea pacis* is characterized by its dense pale petiole scales that reach up to the lower rachis and its almost entire pinnules in distal pinna parts. The species is similar in these aspects to *C. pilozana* M.T.Murillo & J.Murillo and *C. marginalis* (Klotzsch) Domin. *Cyathea pacis* differs from *C. pilozana* and *C. marginalis* in having the larger pinnules strongly pinnatifid (vs. never incised more than  $1/5$  towards the costules). *Cyathea pacis* and *C. pilozana* have hemitelioid indusia whereas *C. marginalis* is exindusiate.

*Cyathea pacis* is yet another example of a newly discovered species that bears a strange combination of characters known from several different species (like *C. chimaera* Lehnert & A.Tejedor). Superficially it resembles Neotropical species of *Sphaeropteris* by its large croziers covered in thin, papery scales. With its hemitelioid indusia and reduced petiole scale margins, it probably

belongs to the alliance of *Cyathea traillii* Domin (Lehnert 2011). These species are understory plants of mostly lower elevations and warmer climates, often occurring on sandstone and similarly nutrient-deficient soils. We do not have any information on the soil chemistry at the type locality, but the bedrocks could be late Cretaceous oceanic basalts, mylonitic schists or sedimentary rocks (Sillitoe and Perello, 2005).

**8. *Cyathea pholidota*** Lehnert, F.Giraldo & A.Tejedor, *sp. nov.* Type: COLOMBIA. Risaralda: Santa Cecilia, vía que conduce desde Pueblo Rico a Santa Cecilia, al borde de la vía principal, 05°19'45.0"N, 76°10'23.72"W, 2000–2160 m, 28 Jul 2015, *Giraldo F. 3132 with A. Tejedor* (holotype: HUA-202172/-202173/-202174!). **Fig. 8.**

Trunks 1.8 m tall, erect to decumbent, to 6 cm diam., without old petiole bases, epidermis shiny black, with groups of sunken orange–brown lenticels (ca. 4–6 × 3–4 mm) below the grayish brown elliptic frond scars; without adventitious buds. Fronds to 200 cm long, arching from erect to ascending petioles. Petioles to 40 cm long, inermous to verrucate, dark brown, matte to weakly shiny, with easily abraded scurf consisting of appressed, light brown dissected squamules and branched hairs, inconspicuous on similar colored epidermis; petioles basally without lenticels or not detectible in dried material; persistently scaly, especially along the margins, scales reaching up to most of the rachis and along the costae. Petiole scales narrowly lanceate, 10–25 × 3–4 mm, shiny, concordantly bicolorous to almost concolorous, brown to dark brown with lighter brown to yellowish white margins, bases cordate, pseudopeltately attached, apices long acute to attenuate, straight to falcate, undulate but not twisted; differentiated margins narrow (ca. 0.2 mm), fragile, often abraded, the cell rows strongly exserted. Laminae to 160 × 130 cm, ovate, bipinnate-pinnatifid, firm-herbaceous, matte, a rich green adaxially, blackish when dried, olive-green abaxially; apices abruptly reduced, ± conform. Rachises inermous, brown to dark brown abaxially and adaxially; adaxially in distal parts short-pubescent with reddish brown multicellular hairs to 1.0 mm long, abaxially with dark brown bullate squamules 0.5–1.0 mm long, hairs absent; larger brown lanceate scales persistent adaxially and along the sides, to 15 × 3–4 mm. Pinnae to 65 cm long, patent to weakly ascending, sessile, 7–8 pairs per frond, subopposite to alternate, inarticulate, narrowly green-alate for most of their length, alae in basal half turned upwards, in distal half patent and visible, distal segments simply adnate before ending in a pinnatifid apical section; basal pinna pairs 1/2–1/3 of the length of the medial pinnae, with cuneate inequilateral bases (basiscopic pinnules absent), reflexed. Costae to 3.0 mm wide, inermous, dark brown on both sides, adaxially with brown, antrorsely curved to appressed, uniseriate hairs to 1 mm long, abaxially with many dark brown bullate squamules (0.4–0.6 mm long) with acuminate tips, with larger flat concolorous brown lanceate scales to 15 × 3 mm, hairs lacking; junctures of costae and rachises abaxially weakly swollen, each with an inconspicuous, planar to weakly protruding, elliptic pneumathode to 6 × 3



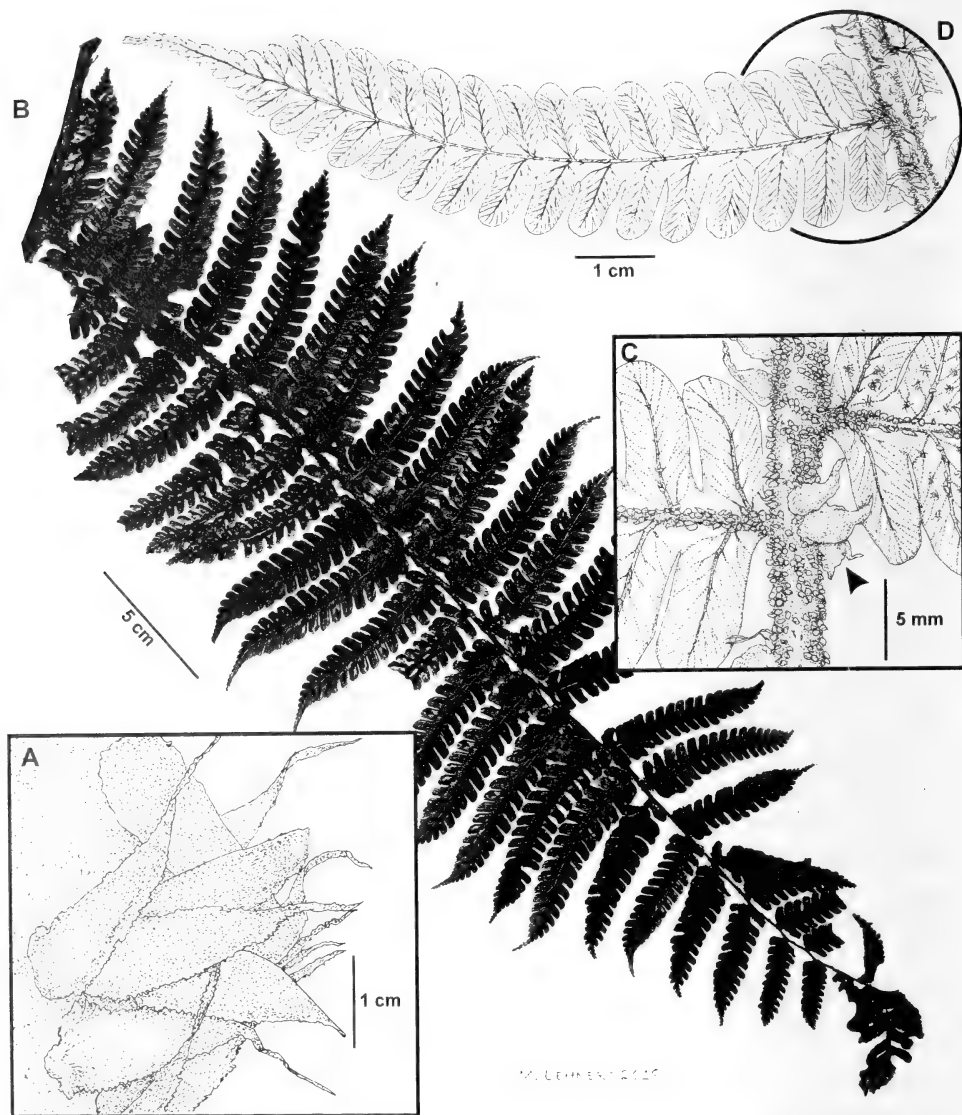


FIG. 8. *Cyathea pholidota*. A. Petiole with scales. B. Pinna. C. Costa and segments abaxially, most sori shown without sporangia; note the abundant bullate squamules on the costa, arrow points to larger persistent scales. D. Pinnule, adaxially (from *Giraldo 3132*, BONN).

mm, basally with a shiny black spot (foliar nectary). Pinnules to  $90 \times 18\text{--}29$  mm, sessile, inarticulate, ca. 18–20 mm between costules, linear-oblong to lanceate, pinnatifid to basally pinnatisect or pinnate, bases truncate to cuneate, tips acute to attenuate (almost caudate in large pinnules) with crenate to serrate margins; costules grayish to greenish brown on both sides, adaxially strongly prominent, ridged, abaxially weakly to strongly prominent, adaxially moderately hairy with tan to brown, curved to appressed, uniseriate hairs 1.0–

1.5 mm long, abaxially without hairs, with many strongly bullate, ovate-acuminate, dark brown squamules with entire margins to 0.5 mm long, also some flat brown scales, these ovate (to ca.  $1 \times 1$  mm) to broad-lanceate (to ca.  $3 \times 2$  mm); costules basally without pneumathodes. Segments to  $11.5 \times 4.0$ – $5.0$  mm,  $\pm$  oblong, sessile, adnate, patent to ascending, distally straight to weakly falcate, tips obtuse to rounded, proximal segments alternate to subopposite, usually as large as the next segments, approximate; sinuses acute (obtuse to rectangular in pinnate parts), 0.5–1.0 mm wide; margins entire to subentire; veins weakly raised adaxially and abaxially (midveins more strongly), greenish to yellowish, ending in the margins, adaxially slightly widened at the tips; veins lacking hairs on both sides or midveins adaxially with single erect, tan to brown, uniseriate hairs 0.5(–1.0) mm long; abaxially with dark brown, weakly to strongly bullate squamules; sterile veins simple or forked, fertile veins mostly forked. Sori 0.8–1.0 mm diam., medial to inframedial,  $\pm$  equidistant between midveins and margins in lower half of segment, slightly closer to midvein in upper half of segment, in the fork of veins, mature dark orange-brown; indusia lacking; receptacles globose, 0.3–0.4 mm diam., not subtended by a scale, paraphyses numerous, straight, pale brown to reddish, of the same length or shorter than the sporangia (0.3–0.4 mm long). Spores not examined.

*Etymology*.—The epithet refers to the persistent, overlapping scales on petioles and frond axes, which resemble the tails of pangolins (order Pholidota, from Greek *φολιδότα* = scale-bearing).

*Distribution and Habitat*.—Western slopes of the Cordillera Occidental in Colombia (Depts. Chocó and Risaralda), in the understory of perhumid forests at 2000–2160 m.

*Additional Specimens Examined (Paratypes)*. COLOMBIA. Chocó: San José del Palmar, Cerro del Torrá, (ca.  $04^{\circ}48'N$ ,  $76^{\circ}30'W$ ) 1940–2160 m, 1 Sep 1988, P.A. Silverstone-Sopkin 4939 (CUVC, F, MO).

*Cyathea pholidota* occurred in a large population at the type locality. It has relatively slender trunks without old petiole bases, showing a shiny black epidermis and reddish lenticels below the frond scars. With its abundant dark brown bullate squamules on the costules and costae, this species may be confused with *C. darienensis*, like was the paratype Silverstone-Sopkin 4939. *Cyathea pholidota* differs in having larger scales on the petioles ( $10$ – $25 \times 3$ – $4$  mm in *C. pholidota* vs.  $10$ – $12 \times 2$ – $3$  mm in *C. darienensis*) that are usually also present and persistent along the rachises (vs. lacking here), and rachises and costae lacking hairs abaxially (vs. inconspicuous short, thin hairs present). *Cyathea pholidota* also has thicker trunks (6 cm diam. vs. 2–3 cm diam. in *C. darienensis*).

9. *Cyathea rengifo* Lehnert, F. Giraldo & A. Tejedor, **sp. nov.** Type: COLOMBIA. Antioquia: Municipio Yarumal, Vereda Alto de Ventana, via que conduce al corregimiento El Cedro,  $07^{\circ}04'22''N$ ,  $75^{\circ}26'23.9''W$ , 1893 m, 20 Jul 2015, F. Giraldo, A. Tejedor, & A. Mejía 3122 (holotype: HUA-2012292/-2012293!, isotype: BONN!). **Fig. 9.**

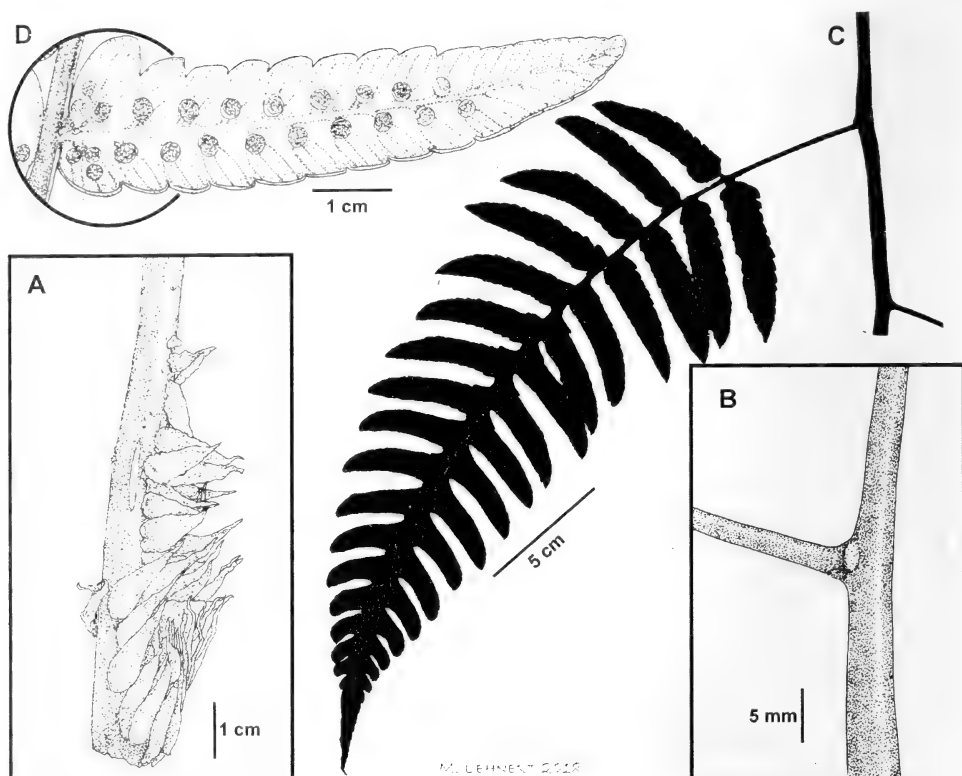


FIG. 9. *Cyathea rengifoii*. A. Petiole with scales. B. Junction between rachis and costa, showing glabrous shiny epidermis and pale pneumathode. C. Pinna. D. Pinnule, fertile, abaxially (from Giraldo et al. 3122, BONN).

Trunkless, rhizomes short-creeping, ca. 13 cm long, to 4 cm diam., covered in old petiole bases and adventitious roots; adventitious buds lacking. Fronds to 210 cm long, arching-drooping from erect to ascending petioles. Petioles to 73 cm long, inermous or sparsely verrucate, dark atropurpureous to black; petioles basally with two lines of large elliptic, pale brown lenticels to  $7.0 \times 1.0$ – $2.5$  mm; without adventitious (aphlebioid) pinnae at the bases; petiole scurf absent or few appressed lacerate brown squamules; larger scales restricted to base, soon caducous. Petiole scales broadly lanceate to ovate,  $5$ – $10$ (– $12$ )  $\times$   $3$ – $4$  mm, shiny dark brown, concordantly bicolorous with very narrow, inconspicuous yellowish to pale brown margins, pseudopeltately attached, their tips straight. Laminae to  $130 \times 70$  cm, long-triangular, pinnate-pinnatifid to bipinnate, with truncate bases and gradually reduced, long tapering apices; chartaceous, glossy dark green adaxially, often blackish when dried, paler green abaxially, pinnae ca. 11 pairs per frond, alternate, not reduced towards base. Frond axes atrovinaceous to black on both sides, adaxially hairy only on costae and distal parts of rachises, hairs  $0.5$ – $1.0$  mm long, tan to brown, axes abaxially completely glabrous or with few evanescent

hairs on rachises; insertions of costae into rachises not or weakly swollen, with one conspicuous pneumathode, pale brown, elliptic, ca.  $3.0 \times 1.5$  mm, area below pneumathode wrinkled (foliar nectary). Largest pinnae  $20\text{--}35 \times 8\text{--}10$  cm, broadly lanceate, pinnatifid to pinnate, basally  $\pm$  truncate, tapering from the middle to short attenuate tips, stalked to 4 cm,  $3.0\text{--}4.5$  cm between the stalks, stalks inarticulate; segments (or pinnules) to  $42 \times 8\text{--}12$  mm, free ones sessile to stalked to 1 mm, margins strongly crenate or lobed to  $1/3$  towards the costules, basally auriculate, acroscopically pronounced, adnate segments basally decurrent into the costae, margins crenate to crenulate; segments (or pinnules) patent to weakly ascending with straight to falcate, acute tips; basal segments (or pinnules) usually alternate to subopposite; sinuses wide, acute to rectangular, to 5 mm wide; veins carneous to blackish, contiguous with the identically colored hyaline segment margins; each midvein insertion with the costae weakly raised, bearing a small elliptic pneumathode  $0.2\text{--}0.3$  mm long; segments adaxially with few to many antrorsely curved multicellular hairs  $0.5\text{--}1.0$  mm long only on the costules, abaxially no hairs on or between the veins, here only small orange-brown bullate squamules to  $0.5$  mm long and round to round-ovate flat scales  $1.0\text{--}1.5$  mm diam., pseudopeltately attached with strongly cordate bases; sterile veins simple or forked, fertile veins forked once or twice. Sori  $1.0\text{--}1.2$  mm diam., subproximal, in fork of veins, deep brown, indusia hemitelioid, brown, persistent, weakly arching, the margins worn off in over-mature sori, reaching  $1/4\text{--}1/3$  around the receptacles, receptacle globose, to  $0.5$  mm diam., paraphyses few, straight to distally curved, brown to red, of the same length as or slightly longer than sporangia ( $0.4\text{--}0.5$  mm). Spores tetrahedral, whitish to pale brown.

*Etymology*.—This species is dedicated to Jorge Wilson Rengifo Moscoso (1960– ), dedicated technician in charge of collections at herbarium HUA, University of Antioquia, Medellín.

*Distribution and Habitat*.—Endemic to northern Colombia at ca. 1800–2000 m, in moist montane forests, growing on roadbanks and cliffs in partial shade.

*Cyathea rengifo* is best described as an indusiate version of *C. latevagans* (Baker) Domin with more strongly dissected laminae (laminae at least partially bipinnate, indusia hemitelioid in *C. rengifo* vs. laminae always pinnate-pinnatifid, indusia lacking in *C. latevagans*) as both species share a trunkless habit with overhanging to dangling fronds, shiny dark frond axes and round, pseudopeltately attached orange scales abaxially on the laminae.

Superficially, *Cyathea rengifo* looks like it might be of hybrid origin. It strongly resembles *C. latevagans*, which is found regularly in the area, but differs in features that lie not within the range of morphological variation typical of that species. Hybrids are documented in the family Cyatheaceae (e.g., Conant, 1975; Caluff, 2002a, b), and may be even fertile in the first generation, as is documented for Caribbean *Alsophila* (Conant and Cooper-Driver 1980). In other genera of Cyatheaceae, hybrids are sterile and produce mostly malformed spores (e.g., Caluff, 2002a). The spores of the only documented specimen of *C. rengifo* are regularly shaped and evenly sized, suggesting that it is not a sterile primary hybrid. Even if its status as a hybrid

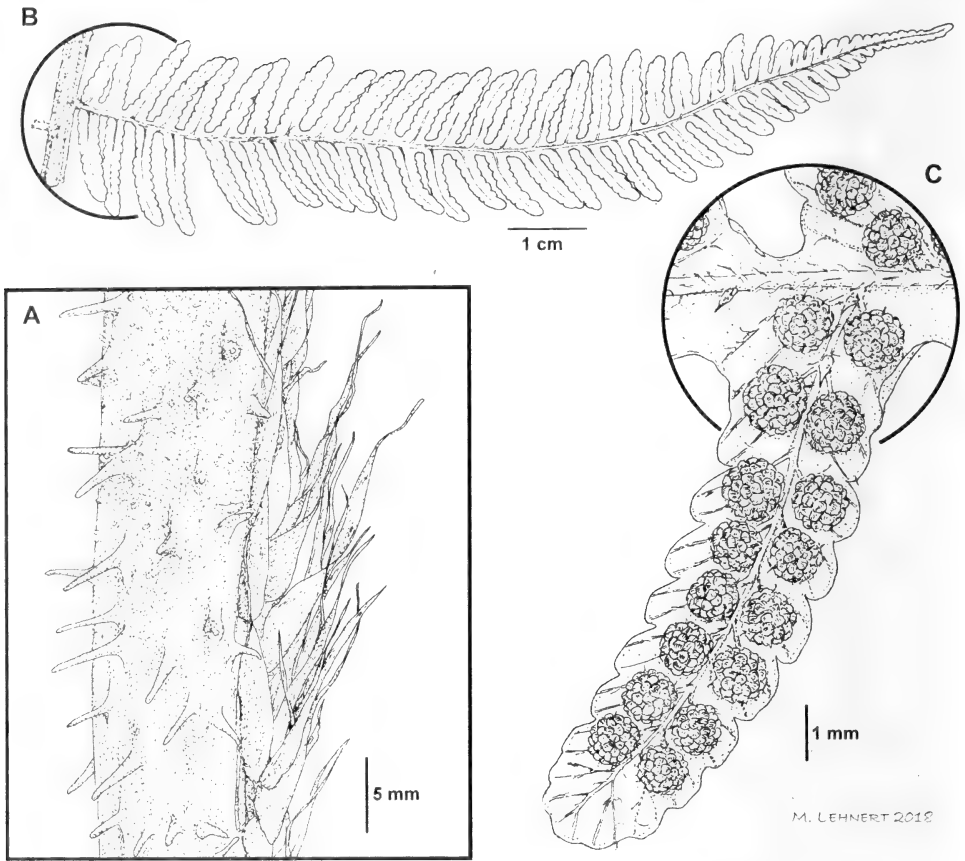


FIG. 10. *Cyathea rodriguezii*. A. Petiole with scales. B. Pinnule, adaxially. C. Segment, fertile, abaxially (from Rivas 781, HUA).

remains dubious, it is a distinct taxon that deserves a formal recognition for further scientific study. A similar case is the herein described *C. toroi* Lehnert, F.Giraldo & A. Tejedor, *sp.nov.*, which see for further discussion.

10. *Cyathea rodriguezii* Lehnert & F.Giraldo, *sp. nov.* Type: COLOMBIA. Antioquia: Caldas, Mun. Samana, margen derecha del Río Moro, sector La Mula, 05°33'48.1"N, 74°54'15.3"W, 550–650 m, Jul 2005, A. Rivas 781 (holotype: HUA-149416/-149351!). Fig. 10.

Trunks to 6 m tall, to 10.5 cm diam., otherwise unknown; adventitious buds not reported. Fronds to 330 cm long. Petioles to 88 cm long, aculeate with many strong prickles to 8 mm long, brown to dark brown, matte; petioles basally covered with orange-brown scurf of small lanceate, flat to weakly bullate squamules to 2 mm long, with few orange-brown lenticels to  $4 \times 2$  mm; scaly in basal half, persistent adaxially and along the sides. Petiole scales

narrowly lanceate,  $10\text{--}12 \times 2.5\text{--}3.0$  mm, weakly shiny, weakly bicolorous, auburn to brown with golden brown to whitish margins, bases cordate, pseudopeltately attached, apices long-acute, straight to falcate, twisted; differentiated margins narrow, persistent, without setae or cilia. Laminae to  $240 \times 125\text{--}150$  cm, bipinnate-pinnatifid, herbaceous, matte, dark green adaxially (olive-green in dried material), pale grayish green abaxially; apices not seen. Rachises ochre to brown abaxially and adaxially, weakly shiny, muricate to sparsely aculeate, with blunt prickles to 2 mm long; adaxially sparsely to densely pubescent with whitish to brown multicellular hairs to 1.0 mm long; abaxially with numerous white spreading, flaccid hairs 1.0–1.5 mm long, with remnants of pale scurf; scales absent. Largest pinnae to 64 cm long, sessile to stalked by 1 cm, ca. 16–20(–26?) pairs per frond, patent weakly ascending, alternate, inarticulate, distally not or only narrowly green-alate, distal segments decurrently adnate before ending in a pinnatifid apical section; basal pinna pairs not seen. Costae to 3 mm wide, dark stramineous to yellowish abaxially, darker brown adaxially, sparsely muricate, prickles 1 mm or less; with whitish, multicellular hairs 1.0–1.5 mm long, adaxially dense, appressed, abaxially sparse, spreading, and ephemeral; sometimes with remnants of scaly scurf; junctures of costae and rachises abaxially weakly swollen, each with a conspicuous, planar to weakly protruding, elliptic aerophore to  $3.5 \times 2.0$  mm. Largest pinnules  $120 \times 35$  mm, sessile to sessile with stalks to 0.5 mm, inarticulate, 2.5–3.0 cm between the stalks/costules, pinnules linear-oblong to lanceate, bases truncate to cuneate, tips short- to long-attenuate, with serrulate to crenulate margins; costules carnes to ochre on both sides, adaxially strongly prominent, ridged, abaxially weakly to strongly prominent, moderately to densely hairy with whitish to tan, multicellular hairs to 1.0(–1.5) mm long, adaxially curved to appressed, abaxially spreading; abaxially with flat brown squamules to  $1.0 \times 0.4$  mm, pale brown to tan bullate squamules to  $2 \times 0.5$  mm, ephemeral tortuous hyaline hairs to 0.6 mm long, and unicellular trichomidia; costules basally without visible pneumathodes. Segments to  $15 \times 2.0\text{--}2.5$  mm, ascending, short ones straight, long ones distally falcate, tips acute to obtuse, proximal segments alternate to subopposite, as large as the next segments, often remote; sinuses acute to obtuse, to 1.0–2.5 mm wide; margins deeply crenulate; margins not differently incised in proximal segments of a pinnule; veins planar to weakly protruding adaxially and abaxially, dark stramineous to blackish, ending in the margins; veins adaxially sparsely to moderately hairy, abaxially abundantly hairs with erect, whitish, multicellular hairs 0.5–1.0 mm long, not between the veins; midveins abaxially with some whitish to pale brown, bullate squamules and some tortuous, appressed hairs; sterile veins simple or forked, fertile veins forked. Sori 0.8–1.0 mm diam., medial to suprmedial, parallel to the midveins, filling out most of the segments, in the fork of veins, mature dark orange-brown; indusia lacking; receptacles globose, 0.2–0.3 mm diam., not subtended by a scale, paraphyses many, basally straight, brown to reddish, distal white, tortuous, longer than the sporangia (0.4–0.5 mm long). Spores not examined (not mature in available material).

*Etymology*.—The species is dedicated to our friend and colleague Wilson Rodríguez Duque (1957– ), Instituto de Investigaciones Científicas Amazónicas-SINCHI, Bogotá.

*Distribution and Habitat*.—Northern Colombia, Depts. Antioquia and Santander, at 550– 1850 m.

*Additional Specimen Examined (Paratype)*. COLOMBIA. Santander: Corregimiento de Virolín, adelante de Bogotácito, (ca. 06°04'19"N, 73°12'21"W) 1800–1850 m, 27 Nov 1978, S. Díaz-P. 1177 (COL).

The present specimens of *C. rodriguezii* are from stout plants with dimensions typical of *Cyathea conjugata* and allies, and the persistent pubescence on the axes combined with the deeply crenate segment margins of *C. rodriguezii* suggest a closer relationship to that group.

*Cyathea rodriguezii* differs from the wide-spread *C. microdonta* mainly in having larger laminae (to 240 × 125–150 cm with 16–20 pinna pairs in *C. rodriguezii* vs. 200 × 120 cm with 10–15 pairs in *C. microdonta*), being hairier abaxially on costules and veins (erect, whitish, multicellular hairs 0.5–1.0 mm long abundantly on veins vs. glabrous to sparsely hairy), and lacking long prickles on the frond axes (inermous, or with few short blunt prickles vs. needle-like prickles to 7 mm long). *Cyathea rodriguezii* probably also grows larger than *C. microdonta* (trunks to 6 m tall vs. trunks to 4 m, usually smaller) but has smaller petiole scales (10–12 × 2.5–3.0 mm vs. 14.0–32.0 × 2.5–4.5 mm). From our experience, *C. microdonta* has slender frond axes that have some weak luster; hairs if present abaxially are easily abraded and leave a smooth surface here. Furthermore, larger plants (> 1.5 m tall) of *C. microdonta* usually sprout small plants from the trunk base, forming small groups. This has not been reported for the specimens of *C. rodriguezii*, and is also unknown from *C. conjugata* and allies.

11. *Cyathea tejedoris* Lehnert, F. Giraldo & W. Rodríguez, *sp. nov.* Type: COLOMBIA. Nariño: Mun. Ricaurte, road between Ricaurte and Junín, 01°10.825'N, 78°06.899'W, 1200 m, 15 Feb 2015, M. Lehnert 3144 with W. Rodríguez, F. Giraldo & M. Kessler (holotype: HUA-198736/-198737/-198738/-198740!, isotypes: BONN!, Z!). **Figs. 11, 12.**

Trunks 0.2 m tall (ascending apex of short-prostrate rhizomes), to 10 cm diam., without old petiole bases, epidermis dark brown, densely covered in linear-lanceate scales, concolorous orange-brown, shiny; apices not hidden in fascicles of petioles; adventitious buds absent. Fronds to 690 cm long, arching from ± patent petioles, soon drooping, scrambling for most of their length. Petioles to 85 cm long, densely short aculeate, prickles 1–3 mm long, epidermis dark brown, weakly shiny, obscured by scurf of orange- to reddish brown lanceate scales with spreading white cilia. Petiole scales ca. 20–35 × 1 mm, linear-lanceolate, mostly curved near the base, ending in an undulate to twisted filiform tip, appearing concolorous orange- to reddish brown, with a narrow white margin with spreading cilia of various length, soon worn off in distal scale parts, more abundant and persistent near the base. Laminae ca. 600



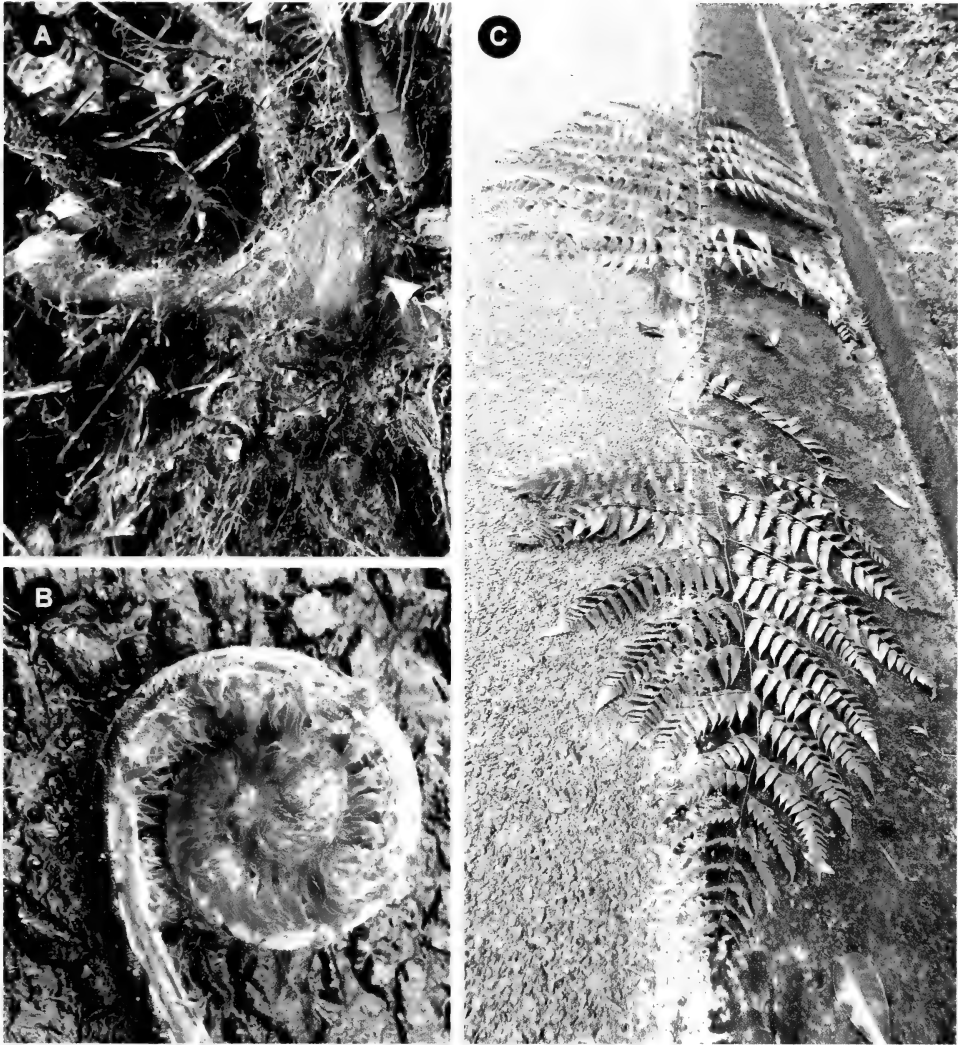


FIG. 11. *Cyathea tejedoris*. A. Trunk, short and erect (ca. 10 cm diam.), excavated from organic debris in which it was growing; note young frond going off at an almost right angle; arrow on the right points to apex. B. Tip of expanding frond (ca. 4 cm diam.); the crozier has shorter and proportionally broader scales than the petiole; note fine white scurf in the coiled-up part. C. Entire frond (690 cm long), central pinnae damaged from extraction from shrubbery through which it was growing (photos from Lehnert 3144).

× 180 cm, bipinnate-pinnatifid to tripinnate, coriaceous, apices gradually reduced. Frond axes including pinnule stalks abaxially short-aculeate, prickles 1–2 mm long, medium to dark brown on both sides, often curved, mostly retrorsely, into a hooked tip; adaxially costules, costae, and distal parts of rachises with antrorsely curved multicellular hairs 1.0–1.5 mm long, tan to brown on rachises, white to tan on costules and costae, hairs lacking abaxially;

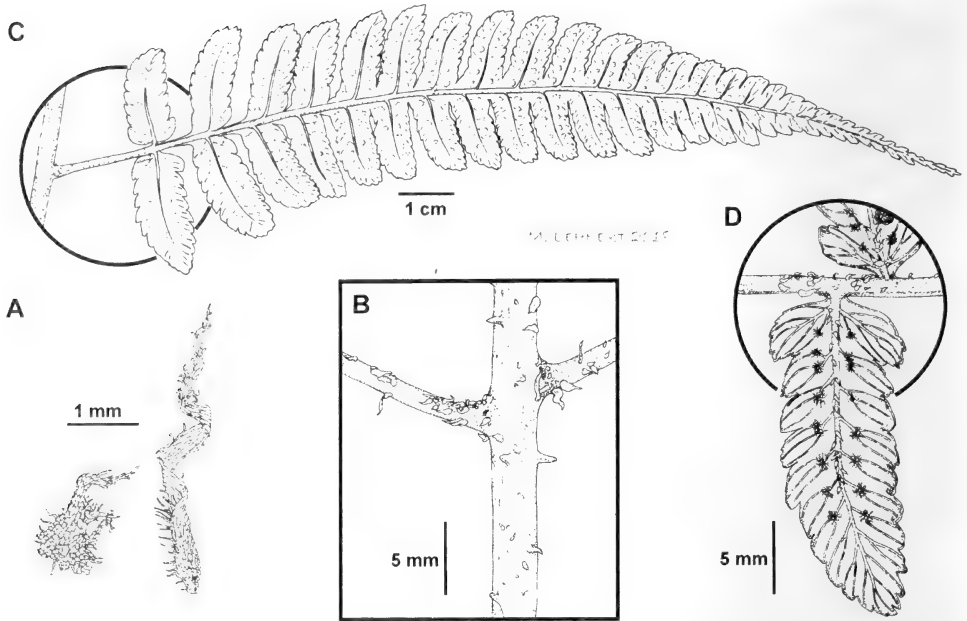


FIG. 12. *Cyathea tejedoris*. A. Smaller petiole scales; similar scales also persisting on frond axes. B. Rachis and costae, showing persisting smaller scales and the prickles on the rachis. C. Pinnule, adaxially. D. Segment, fertile, abaxially (from *Lehnert 3144, BONN*).

remnants of scurf (including some larger scales to ca.  $10 \times 2$  mm) persisting in axils of rachis, costae and costules, otherwise costae abaxially with few flat lanceate scales, costules with few to many dark reddish brown to castaneous bullate squamules to  $0.7 \times 0.5$  mm, with either subulate or flattened, lacerate tips; junctions of costae and rachises swollen, abaxially with 1–3 flat to weakly sunken, round to ellipsoid pneumathodes to  $3.0 \times 1.5$  mm, intruding or embedded in darker spot ca.  $5 \times 3$  mm (foliar nectary). Pinnae to 90 cm long, lanceate, alternate,  $\pm$  patent, 22–24 pairs per frond, stalked to 9.5 cm, basal ones  $\pm$  half the size of largest pinnae, weakly reflexed. Pinnules to  $200 \times 43$  mm, long-triangular to lanceate, tapering from the base or below the middle to attenuate or caudate tips with serrate margins, most pinnules long-stalked to 3 cm with cordate bases, smaller ones sessile with rounded bases, all well-spaced (to 5 cm between pinnule stalks), not overlapping; segments to  $25 \times 10$  mm, sessile and adnate except for the lower ones of large pinnules, these free, sessile to subsessile, lanceate with prominent basal lobes, grading from basally contracted to basally decurrent segments towards the pinnule tips, all weakly ascending and weakly falcate, their tips obtuse to short acute, sinuses to 8 mm wide, obtuse with  $\pm$  parallel sides, margins flat, sharply crenate along sinuses, serrulate at tips. Veins yellowish brown adaxially and darker brown abaxially; midveins strongly, lateral veins weakly protruding on both sides, midveins of largest segments adaxially with few multicellular hairs, otherwise veins

lacking hairs, midveins abaxially with few to many dark reddish brown to castaneous bullate squamules to  $0.7 \times 0.5$  mm, with either subulate or flattened, lacerate tips, in larger segments also with few flat scales to  $1.5 \times 0.7$  mm; sterile veins forked or simple, fertile veins forked 1–2(–3) times. Sori 1.2–1.5 mm diam.,  $\pm$  medial, in fork of veins; indusia lacking; receptacles globose to elliptic, 0.4–0.5 mm in diameter; paraphyses numerous, laterally flattened with a thin subulate terminal cell, dark reddish brown, longer than the sporangia (0.5–0.6 mm). Spores not examined.

*Etymology*.—The specific epithet honors our friend and colleague Adrian Tejedor (1975–), who discovered the species. The family name is here treated as being already Latin, belonging to the consonantic declination (-or, gen. -oris).

*Distribution and Habitat*.—Southwestern Colombia (Chocó region) in wet lower montane forests at 1000–1200 m, growing on ridges with low open canopy and dense shrubby undergrowth.

*Additional Specimen Examined (Paratype)*. COLOMBIA. Nariño: Junín, 5 km en dirección a Barbacoas, 1000 m, 12 Dec 1972, W. Hagemann & N. Leist 1728 (COL).

At first sight, *Cyathea tejedoris* resembles *C. gibbosa* H.Karst (previously known as *C. kalbreyeri* (Baker) Domin; Lehnert, 2014) by exceptionally long fronds, coriaceous laminae, long-stalked long-triangular pinnules and the narrow orange-brown petiole scales. Under closer inspection, however, the spiny axes and patent petiole bases distinguish *C. tejedoris*: in *C. gibbosa*, the axes are inermous and the petiole bases appressed to the trunk. In contrast to *C. tejedoris*, whose fronds scramble through the lower shrubby vegetation, *C. gibbosa* usually grows under a taller canopy, where its crosiers first grow up erectly until they find support on a higher tree branch, from where the hanging frond starts to unfurl completely. Because of the prickles on the petioles and axes, *C. tejedoris* may be confused with *Cyathea nodulifera* R.C.Moran, a potentially sympatric species (Moran, 1991), but differs from it in the long-scrambling fronds, the lack of trunks and the green epidermis of petioles and axes (vs. fronds upright and arching, trunks present, epidermis mostly dark brown to atropurpureous or black in *C. nodulifera*).

*Cyathea tejedoris* can be distinguished from further species with similarly long-stalked long-triangular pinnules either by the shape and color of the petiole scales (linear-lanceolate, shiny orange-brown with white marginal cilia in *C. tejedoris* vs. broader, darker and lacking cilia in *C. gracilis* Griseb. and *C. longipetiolulata* A.Rojas & A.Tejedor) or the absence of indusia (vs. present in *C. divergens* Kunze, *C. gracilis*, *C. longipetiolulata* and *C. meridensis* H.Karst.).

The long-scrambling fronds of *C. tejedoris* with relatively thin rachises, prickles with hooked tips along nearly the entire length of the axes abaxially, plus the short trunk with remotely set petiole bases and an apparently fast growing apex, all seem to be adaptations to life in scrubby vegetation where the fronds themselves have a partially climbing function. This new species is fairly abundant at the type locality. The plants were of various sizes, most of them fertile but none of them with a discernible trunk. The ascending tip of the

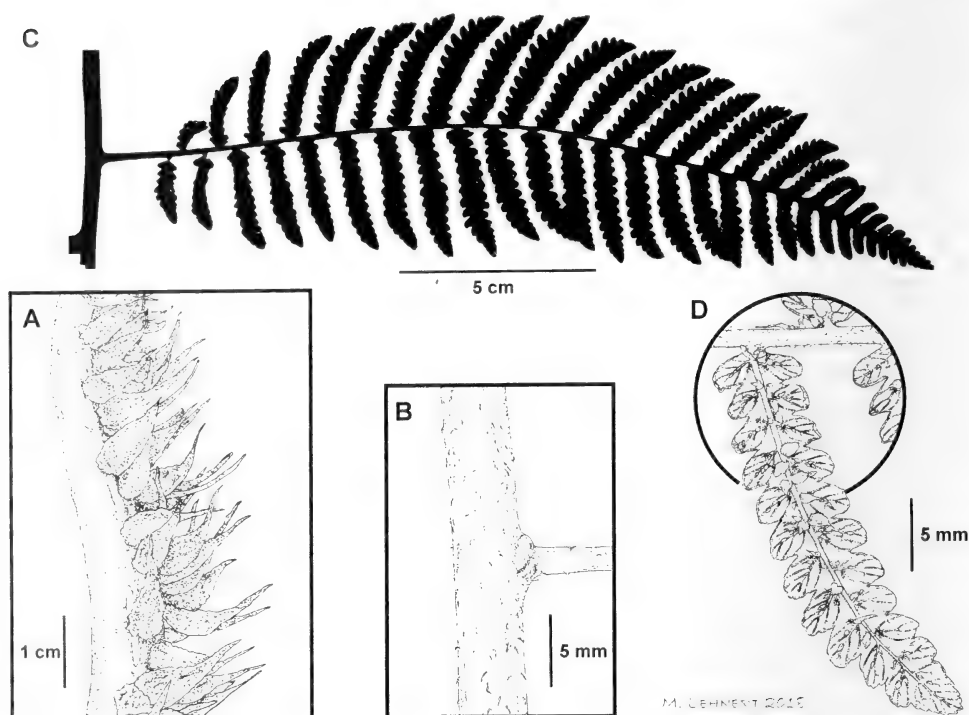


FIG. 13. *Cyathea toroi*. A. Petiole with scales, showing two white pneumathodes. B. Junction of rachis and costa, showing sparse hairy indument and pneumathode. C. Pinna. D. Pinnule, fertile, abaxially (from Giraldo 3127, BONN).

trunk (or rhizome) just elevates the apex with the crosiers over the thick organic litter. *Cyathea tejedoris* grows together with *C. hemiepiphytica* R.C.Moran and *C. brunnescens* (Barrington) R.C.Moran, two other endemics of the Chocó region (Moran, 1991). These two exindusiate species are easily distinguished from *C. tejedoris* by longer, ascending to erect trunks and much shorter fronds (<2 m long).

12. *Cyathea toroi* Lehnert, F.Giraldo & A. Tejedor, *sp. nov.* Type: COLOMBIA. Antioquia: Municipio Yarumal, Vereda Alto de Ventanas, via que conduce al corregimiento El Cedro, 07°04'22"N, 75°26'23.9"W, 1893 m, 20 Jul 2015, F. Giraldo 3127 with A. Tejedor, A. Mejia (holotype: HUA-202297/-202298/-202299!, isotype: BONN!). Fig. 13.

Trunks to 0.6 m tall, 9 cm diam., with persisting old petiole bases; trunk apices hidden in fascicles of petioles; adventitious buds lacking. Fronds to 305 cm long, arching from erect petioles, drooping from the middle. Petioles to 74 cm long, inermous to sparsely verrucate, atropurpureous, basally blackish, on each side with an interrupted line of white lenticels, each to  $7 \times 1$  mm; scurf lacking; without adventitious (aphlebioid) pinnae at the petiole bases; petiole

scales only near base and easily shed, often missing in dried material. Petiole scales broad-lanceate to ovate-lanceate,  $15\text{--}20 \times 2.5\text{--}3.5$  mm, their tips straight to falcate, almost concolorous to concordantly bicolorous, the dark brown to castaneous center grading into the orange-brown to yellowish margins, lustrous. Laminae to  $230 \times 55$  cm, bipinnate-pinnatifid, herbaceous, widest at the middle, apices gradually reduced; dark green adaxially, blackish when dried, olive-green abaxially. Frond axes inermous, atropurpureous, hairs adaxially densely on costules and costae, sparsely to absent in most parts of rachises, hairs 0.5 mm long, tan to brown, antrorsely curved, abaxially glabrescent with few spreading white hairs to 1.5 mm long; flat orange-brown scales sparsely on costae, sparse to abundant on costules abaxially, scales lanceate (to  $3 \times 2$  mm) and round-ovate (1.0–2.5 mm diam.); junctures of costae and rachises abaxially not or weakly swollen, each with a weakly raised, elliptic pneumathode to  $3.0 \times 1.5$  mm, pale brown, basally with a black area (foliar nectary), appearing corrugated, often sunken in. Pinnae to 27 cm long, ca. 14–16 pairs per frond, alternate (basal ones also subopposite to opposite), stalked 2–3 cm, narrowly green-alate in distal half, the alae concave, the distal segments weakly decurrently adnate. Largest pinnules  $33 \times 8$  mm, pinnules linear-oblong to weakly oblanceate, truncate to weakly rounded at base, tapering from beyond the middle to acute tips, sessile to stalked 1 mm, 8–11 mm between the stalks/costules, alternate; pinnules incised to  $2/3$  towards the costules, ca. 1.5 mm distance below the sinuses; segments to  $4 \times 2$  mm, patent to weakly ascending, weakly falcate towards their rounded to obtuse tips, with subentire to crenulate margins, sinuses 0.5–1.0 mm wide, acute, triangular, open. Veins glabrous adaxially except for few whitish, erect multicellular hairs to 1 mm long on the midveins; abaxially with scattered white hairs 0.5–1.0 mm long on veins and midveins, few also between the veins; midveins abaxially with orange-brown to auburn bullate squamules 0.5–1.0 mm long with rather short tips and entire margins, equally sized flat squamules with attenuate to caudate tips and lacerate margins; sterile and fertile veins simple, rarely forked. Sori ca. 0.8 mm diam., each with fewer than 20 sporangia, subproximal, on the back of veins; indusia absent; receptacles globose, 0.2–0.3 mm diam., sometimes subtended by a brown lacerate squamule; paraphyses often apically tufted, hyaline, tan to brown, of the same length or longer than sporangia (0.3–0.4 mm), the distal parts often broken off in over-mature sori and then shorter than sporangia. Spores not examined.

*Etymology*.—The species is dedicated to Juan Lázaro Toro Murillo (1966–), expert on Colombian ferns.

*Distribution and Habitat*.—Known only from the type locality in northern Colombia, Dept. Antioquia, at 1893 m.

*Additional Specimen Examined (Paratype)*. COLOMBIA. Antioquia: Municipio Yarumal, Vereda Alto de Ventanas, via que conduce al corregimiento El Cedro,  $07^{\circ}04'22''\text{N}$ ,  $75^{\circ}26'23.9''\text{W}$ , 1893 m, 21 Jul 2015, F. Giraldo, A. Tejedor, & A. Mejía 3128 (HUA).

*Cyathea toroi* may be mistaken for a small plant of *C. lechleri* Mett. or *C. delgadii* but it differs by atropurpureous petioles and axes (vs. pale to dark

brown in *C. lechleri*, only petiole base blackish in *C. delgadii*), evanescent petiole scales (vs. scales persisting at least at petiole base in *C. lechleri* and *C. delgadii*), long-drooping fronds (vs. patent-arching), and lacking indusia (rarely some sori subtended by a small scale vs. indusia sphaeropteroid). From *C. rengifo*, which is similar regarding size, shape, texture, and color of the fronds, it differs by most pinnae being sessile to subsessile (only lowest 2 or 3 pairs with stalks 2–3 cm long in *C. toroi* vs. almost all pinnae stalked, stalks to 4 cm long in *C. rengifo*) and lacking indusia (vs. hemitelioid indusia present).

Regarding the drooping fronds, the shiny axes, and the round orange scales on the laminae, this taxon is similar to the trunkless exindusiate *Cyathea latevagans*. The latter species can be found frequently in the northern Andes, and also occurs close to the type locality of *C. toroi*. The distinctive shape of the pinnae of *C. toroi* (Fig. 13C) is reminiscent of documented hybrids in Cyatheaceae between species with pinnate-pinnatifid and bipinnate-pinnatifid fronds. A good example is *Cyathea*  $\times$  *hombersleyi* from Trinidad (Caluff, 2002b), in which whole pinnae as well as most of the pinnules are slightly oblanceate, and also more strongly incised towards their respective tips (see representative specimen at <http://apps.kew.org/herbcat/>; barcode=K000589789). Aborted sporangia and malformed spores are generally indicators of hybrids in ferns. The available specimens of *C. toroi* had most sporangia and all spores shed, which may be interpreted as result of unproblematic regular sporulation. Hence we treat *C. toroi* as a natural species until the results of our ongoing molecular studies on the family may indicate otherwise.

#### Reinstated Species

13. ***Cyathea boconensis*** H.Karst., Linnaea 28. 458. 1856; Fl. Col. 2: 171, t. 190. 1869. Type: VENEZUELA. Mérida: “Habitat ad pedem australis montis glacialis Meridensis altitudine 1000 m”, *H. Karsten s.n.* (B-20\_0131345!, LE-00008027 [image!]). **Fig. 14.**

Trunks to 5 m tall, erect, to 25 cm diameter, without old petiole bases in large plants, variously persistent in smaller ones, trunk apices hidden in fascicles of petioles, sometimes with skirts of dead fronds if growing in dense understory; adventitious buds absent. Fronds 100–350 cm long, weakly arching, patent in large plants, ascending in small ones. Petioles to 76 cm long, muricate to short-aculeate, prickles to 2 mm long, epidermis dark stramineous to brown, basally reddish brown, weakly shiny, densely covered with persistent dark brown scurf consisting of erect lanceate squamules ( $\leq 1$  mm) with crested tips and lacerate margins; without adventitious (aphlebioid) basal pinnae. Petiole scales narrowly lanceate, 25–36(–40)  $\times$  2–3 mm, with elongate, strongly twisted tips (3–4 times, especially when dried), brown to dark brown with somewhat paler margins, but never strongly bicolorous. Frond axes (rachises, costae, costules) inermous, or rachises basally sparsely muricate, yellowish brown to stramineous, with remnants of scurf consisting of pale brown lacerate squamules and branched hairs, in the axils also larger

FIG



*Cyathea boconensis* (Hb. K.)

FIG. 14. *Cyathea boconensis*. Background: Entire plant (strongly reduced). 1. Lower half of medial pinna, adaxially (1×). 2. Fertile pinnule, abaxially (1×). 3. Fertile segments, adaxially (4×). 4. Fertile segments, abaxially (4×). 5. Segment with two sori, transverse section (50×). 6. Crozier with scales removed, showing the prominent aerophores at the insertions of the costae (ca. 0.25×). 7. Scales from lamina (1×) 8. Scales from rachis (15×), with detail of tip of scale 9 (75×). 10. Scale from midvein of segment. 11–12. Pedicellate bullate squamules from veins. 13. Sporangia. Original illustration (Karsten 1869).



ribbon-like and lanceate scales, pale brown to 5 mm long; costae to 3.5 mm wide; antrorsely curved, brown hairs 0.5–1.0 mm long present adaxially only at distally, absent abaxially. Laminae to  $270 \times 120$  cm, bipinnate-pinnatifid, broadly ovate, deep green and lustrous adaxially, paler and matte abaxially, apices gradually reduced. Pinnae to 60 cm long, stalked to 3 cm, alternate, ca. 13 pairs per frond; distally green-alate, the distal segments simply adnate to weakly decurrently adnate; basal pinnae ca.  $2/3$  the length of longest pinnae, weakly reflexed. Largest pinnules  $10.0\text{--}12.5 \times 1.8\text{--}2.1$  cm, linear-lanceate to long-triangular, sessile or subsessile (stalked to 1 mm), bases truncate to weakly cuneate, never with auricles, tips long-acuminate to attenuate with crenulated margins; segments to  $13 \times 3.5\text{--}4.0$  mm,  $\pm$  oblong, weakly ascending, straight to weakly falcate distally, with crenulate to crenate margins and obtuse tips. Veins glabrous adaxially except for few scattered hairs (0.5–0.8 mm long) on midveins, abaxially moderately hairy with white erect to appressed hairs 0.4–0.8 mm long, few also between the veins, veins abaxially with some pale brown, shiny bullate squamules to  $1.0 \times 0.5$  mm, inserted on short pedicel and with long, often filiform apex (non-pedicellate and flat squamules of equal size also present but less frequent); midveins may have ephemeral whitish to tan scurf, similar to scurf on costae and costules; sterile veins simple to forked, fertile veins forked. Sori (0.7–)1.0–1.2 mm diam., subproximal to inframedial, in fork of veins; indusia sphaeropteroid, with umbo, tan to brown, translucent, fragmenting, usually umbo missing at maturity, but cup-shaped part remaining; receptacles globose, 0.2–0.3 mm diam., paraphyses few, hyaline, tan to white, shorter than the sporangia (0.2–0.3 mm). Spores tetrahedral-globose, orange; perispore not examined.

*Distribution and Habitat.*—Northern Colombia (Depts. Boyacá and Santander) and Venezuela (Prov. Mérida) in lower to upper mountain forests at (1000)1500–3033 m.

*Specimens Examined.* COLOMBIA. Boyacá: Vereda La Chapa, Reserva Rogitama,  $05^{\circ}47'41.7''\text{N}$ ,  $73^{\circ}27'23.6''\text{W}$ , 2400–2450 m, 03 Mar 2019, *Lehnert M. 3666 with J. Pinto, F. Giraldo Gallego* (BONN, HUA, M), *ibid.*,  $05^{\circ}47'47.2''\text{N}$ ,  $73^{\circ}27'26.5''\text{W}$ , 2500 m, 04 Mar 2019, *Lehnert M. 3672 with J. Pinto, F. Giraldo* (BONN, HUA, M). Santander: Limites entre Municipios Toná y Pie de Cuesta, bajando del Paramo de Berlín hacia el sector de La Nevera,  $07^{\circ}06'05''\text{N}$ ,  $72^{\circ}59'29''\text{W}$ , 3033 m, 05 Jul 2015, *F. Giraldo, A. Tejedor, & A. Mejía 3076* (HUA-202043/-202044/-202045); Vereda Campamento, Finca of Mónica Macía, coming from Santa Elena, Boyacá,  $05^{\circ}58.265'\text{N}$   $73^{\circ}08.952'\text{W}$ , 2720 m, 06 Mar 2019, *Lehnert M. 3695 with J. Pinto, F. Giraldo Gallego* (BONN, HUA, M)

*Cyathea boconensis* is characterized by the combination of unique pedicellate bullate squamules abaxially on the veins and by short paraphyses. These characters were illustrated by Karsten (1869) and are not found in any other *Cyathea* species with sphaeropteroid indusia, a group that is most abundant and diverse in Andean forests. The illustrated type specimen (Karsten, 1869; Fig. 14) differs slightly in the documented indument (no hairs abaxially as in our specimen, but more of the larger scales persisting on the axes than in our plant) and significantly in the elevation (1000 m vs. 2450–

3033 m). All this may reflect the natural variation of the species. Regarding the elevation, it is likely that the true type locality may be situated a little higher: Mérida is located at a valley bottom at 1000–1200 m but the closest town named Bocono (ca. 8°33'40"N 71°16'49"W) lies at 1500–1600 m.

*Cyathea boconensis* was regarded as a dubious species (Lehnert, 2009) because no recent collections were available. The illustration (Karsten, 1869) without clear reference to the natural colors of the scaly indument could also represent a form of *C. patens* Mett. or *C. frondosa* H.Karst. The type fragment at B does not show the characteristic pedicels in the bullate squamules but short appressed hairs abaxially on the veins, two features that are in conflict with the illustrations. However, the sori in the type fragment are clearly remote from the midveins, as also seems to be the case in our specimen; due to the fragmented indusia, the midveins are now covered in our specimen but the insertion of the receptacles indicates a medial position. We assume that the Berlin material represents pinnules from the more distal parts of the fronds where the indument is usually less developed and more easily worn off. We had no chance to examine the ampler specimen at LE in order to decide if it would serve as the better lectotype. For the time being we regard *C. boconensis* sufficiently supported by Karsten's (1869) illustration and the existence of morphologically matching plants in the wild.

14. *Cyathea clandestina* Lehnert, F.Giraldo & A.Tejedor, **nom. nov.** for *Alsophila crassa* H.Karst., Fl. Columb. 2: 187, t. 199. 1869, not *Cyathea crassa* Maxon, Contr. U.S. Natl. Herb. 13: 40. 1909. *Trichipteris crassa* (H. Karst.) R.M.Tryon, Contr. Gray Herb. 200: 45. 1970. Type: VENEZUELA. Mérida: "Habitat silvas Merida humidus frigidus montium Meridensis altitudine 2000 m", 1859, *F. Engel s.n. (136)* (holotype: B\_20\_0000326!).

**Fig. 15.**

Trunks to 4 m tall, to 13 cm diam., without old petiole bases in large plants, variously persistent in smaller ones, trunk apices hidden in fascicles of petioles, usually with skirts of dead fronds below the crown; adventitious buds absent. Fronds 160–200 cm long, weakly arching. Petioles to 30 cm long, muricate to short-aculeate, prickles to 2 mm long, epidermis dark stramineous to brown, scurf relatively long lasting between prickles, in lower parts consisting of pale brown to whitish, erect squamules ( $\leq 1$  mm) with crested to lacerate margins, grading in distal petiole parts into small well-spaced squamellae with small brown bodies and long twisted hyaline marginal cilia; without adventitious (aphlebioid) basal pinnae. Petiole scales narrowly lanceate, 25–50  $\times$  2.5–3.5 mm, with elongate, strongly twisted tips (3–4 times, especially when dried), brown to dark brown with paler brown to whitish margins, but never strongly bicolorous. Frond axes (rachises, costae, costules) inermous, or rachises basally sparsely muricate, yellowish brown to stramineous, with remnants of scurf consisting of pale brown lacerate squamules and branched hairs; costae to 3.5 mm wide; antrorsely curved, white hairs 0.5–1.0 mm long present adaxially throughout, absent abaxially.



FIG. 15. *Cyathea clandestina*. Background: Entire plant (strongly reduced); medial pinna (1×). 1. Fertile segment, abaxially (ca. 3×). 2. Sorus, longitudinal section, with paraphyses (ca. 50×). 3. Sporangia (ca. 50×). 4. Spores. Original illustration of *Alsophila crassa* (Karsten 1869).

Laminae to  $170 \times 100$  cm, bipinnate-pinnatifid, ovate-elliptic, deep green and lustrous adaxially, paler and matte abaxially; apices gradually reduced. Pinnae to 50 cm long, subsessile to stalked to 1 cm, alternate, 10–12 pairs per frond; distally green-alate, the distal segments adnate, perpendicular to weakly decurrent; basal pinnae ca.  $1/2$  the length of longest pinnae, weakly reflexed, their proximal basiscopic pinnules usually not developed. Largest pinnules  $8.5\text{--}10 \times 1.4\text{--}2.1$  cm, pinnules linear-lanceate to long-triangular, sessile or subsessile (stalked to 1 mm), to 15 mm between the costules/stalks, pinnule bases truncate to weakly rounded, never with auricles, tips long-acuminate to attenuate with crenulated margins; segments to  $8 \times 2.5\text{--}3.5$  mm,  $\pm$  oblong, weakly ascending, straight to weakly falcate distally, with crenulate to crenate margins and obtuse tips. Veins glabrous adaxially except for few scattered hairs (0.5–0.8 mm long) on midveins, abaxially moderately hairy with white erect to appressed hairs 0.4–0.8 mm long, few also between the veins; veins abaxially with some pale brown, matte flat squamules  $0.5\text{--}1.5 \times 0.5$  mm with lacerate margins, few squamules also covering some sori, bullate squamules absent; sterile veins simple to forked, fertile veins forked. Sori (0.7–)1.0–1.2 mm diam., subproximal to inframedial, in fork of veins, with ca. 80–100 sporangia; exindusiate; receptacles globose, 0.3–0.4 mm diam., paraphyses few, hyaline, pale brown to white, slender, shorter than the sporangia (0.2–0.3 mm). Spores tetrahedral-globose, pale yellow; exospore verrucate, perispore not examined.

*Etymology*.—The name refers to the fact that species had been hidden (Latin, *clandestinus*) in the *nomina incertae sedis* because no complete specimens were available to researchers in the past (Barrington, 1978) and the species could not be verified to be distinct.

*Distribution and Habitat*.—Northern Colombia (Dept. Magdalena) and Venezuela (Prov. Mérida) in lower mountain forests at 1500–2000 m.

*Specimens Examined*. COLOMBIA. Magdalena: Santa Marta, Corregimiento Minca, camino que conduce al Cerro de San Lorenzo y Cerro Kenedy,  $11^{\circ}01'51''\text{N}$ ,  $74^{\circ}01'23''\text{W}$ , 1500–1700 m, 26 Jun 2015, F. Giraldo 3056 (BONN, HUA).

VENEZUELA. Mérida: Mérida, H. Karsten s.n. (199) (B?, LE-00008095 [image]).

It would appear that the Engel specimen labelled as holotype at Berlin could not be the type material of *Alsophila crassa* because it was collected in 1889, postdating the publication of the species by 20 years. We think, however, that the date on the label should read 1859 because it is visible that the first “8” has a different stroke than the following number. This would put the collection date during the period of Franz Engel’s travels in Venezuela and New Grenada (1857–1863), just after Hermann Karsten left in 1856.

The specimen in question has two more old handwritten labels besides the one stating “Venezuela, 1859, leg. Engel”. One says “136. *Alsophila crassa* spec. nov., *paleolatae* Mart. affine sed calva, Merida”, and the other one “indusii nullum vestigium, paraphyses elongatis indivisae”. The former could be an original label by Engel; it differs in handwriting from the other two. The

label information about the plant (*i.e.*, similar to *A. paleolata* Mart. [= *Cyathea phalerata* Mart.] but glabrous; no trace of indusium, with long undivided paraphyses) is repeated in Karsten's description, but not verbatim and without reference to Engel as collector.

*Cyathea clandestina* resembles several other Andean *Cyathea* species regarding the apparent lack of hairs on the lamina while having triangular, well-spaced pinnules. Some of these similar species can be easily separated by the presence of indusia that remain as large fragments, often bearing an umbo (*e.g.*, *C. divergens*, *C. meridensis*), or remaining at least as a small lacerate ring around the receptacle (*e.g.*, *C. boconensis*, *C. caracasana* (Klotzsch) Domin, *C. crenata* Christ, *C. cystolepis* H.Karst., *C. tungurahuae* Sodiro). *Cyathea caracasana* and *C. crenata* further differ in having scurf on petioles and laminae that appears castaneous en masse (actually consisting of bicolorous squamellae with dark teeth and pale brown bodies); *Cyathea crenata* also has some of the larger ovate flat laminar squamules bicolorous with castaneous center, white margins and dark brown teeth (vs. laminar squamules colorous to weakly bicolorous without teeth in *C. clandestina*).

*Cyathea clandestina* grows in the same area and vegetation zones as *C. boconensis* and *C. farinosa* (H.Karst.) Domin (syn. *C. gibbosa* auct., non (Klotzsch) Domin; Lehnert, 2014); all three species seem to be restricted to the mountain ranges of northeastern Colombia and northern Venezuela. *Cyathea boconensis*, an indusiate species but otherwise very similar to *C. clandestina*, can be distinguished when sterile by its characteristic pedicellate bullate squamules on the segments abaxially (vs. no bullate squamules present in *C. clandestina*). *Cyathea farinosa*, which is also exindusiate, can be distinguished by weakly bullate, dark brown to castaneous squamules abaxially on costae and costules (vs. no bullate squamules present in *C. clandestina*), and relatively thick reddish paraphyses (vs. slender pale brown paraphyses).

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## Taxonomic Revision of *Cyathea*, Clade *Hymenophyllopsis* (Cyatheaceae)

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**ABSTRACT.**—We present a taxonomic revision of *Cyathea*, clade *Hymenophyllopsis*, a monophyletic group restricted to the tepuis of the Guiana Shield, a region in northern South America. We recognize fifteen species, including four newly described here: *C. indefinita*, *C. minima*, *C. pseudoctenitoides*, and *C. tatei*. The main diagnostic characters for the species are: rhizome (symmetry and scales), lamina division (pinnatisect to 5-pinnate), pinnae (congested or sparse, recurved to ascending), scales and/or hairs of the rachis (shape, size, margins), as well as the shape and margin of the indusium (bivalvate or cyatheoid, entire to deeply lacerate). An identification key, descriptions, taxonomic comments, illustrations, and geographical distribution maps for all recognized taxa are provided.

**KEY WORDS.**—Cyatheales, Guiana Shield, *Hymenophyllopsis*, taxonomy, Tepui

The tepuis are extensive mountain ranges, more or less flat-topped, that can reach about 1000 km<sup>2</sup> in area and 3000 m in elevation (Huber, 1995a). Due to their isolation they can be considered ecological islands, where several endemic taxa occur (Huber, 1988; Lindorf, 2006; Aubrecht *et al.*, 2011). For lycophytes and ferns the tepuis region has relatively high percentage of endemism (Tryon, 1972; Smith, 1995). According to Smith (1995), in the Guiana Shield occur 671 species of ferns and lycophytes and among them 144 species (22%) are endemic. Among the endemic ferns are those long-treated in the genus *Hymenophyllopsis* K. I. Goebel (e.g., Goebel, 1929; Lellinger 1984). Another genus with notable endemism in this region is *Pterozonium* Fée (14 spp. in total and 11 are endemic) (Smith, 1995).

*Hymenophyllopsis* was considered to belong in its own family, Hymenophyllopsidaceae (Pichi Sermolli, 1970; Tryon and Tryon, 1982; Lellinger, 1995), until the molecular and morphological studies by Korall *et al.* (2006, 2007) and Janssen *et al.* (2008), demonstrated that this genus was embedded in Cyatheaceae (Smith *et al.*, 2006). With the other members of Cyatheaceae,

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*Hymenophyllopsis* species share the presence of scales on the rhizomes and on the base of the petioles, sporangia with an oblique annulus in relation to the pedicel, and spores with verrucate ornamentation.

Based on these previous studies, Christenhusz (2009) considered *Hymenophyllopsis* a subgenus of *Cyathea*. However, we do not adopt this circumscription, because Weigand and Lehnert (2016) verified that if the *Hymenophyllopsis* species are excluded, the remaining *Cyathea* taxa do not constitute well-defined subgenera. Thus, in the present paper, we adopt the informal term “*Cyathea* clade *Hymenophyllopsis*” originally suggested by Korall *et al.* (2006, 2007) and Janssen *et al.* (2008).

The last study that included all taxa of the *Hymenophyllopsis* clade was carried out more than 30 years ago by Lellinger (1984), who recognized eight species for this group. Since that time, Maciel *et al.* (2017) described three new species from the tepuis of Venezuela and Brazil, bringing the *Hymenophyllopsis* species total to 11 species, all restricted to the Guiana Shield, where they usually grow in the cracks of sandstone rocks, at high elevations (Maciel *et al.*, 2017). The species can be recognized by the generally erect rhizomes that are covered by scales, delicate, membranaceous and finely dissected leaves up to 30 cm long, varying from pinnate to pinnatisect, with sori at the apex of the veins, protected by a bivalvate or cyatheoid indusium (Lellinger, 1984; Maciel *et al.*, 2017).

The objective of this study is to present the taxonomic revision of the species of *Cyathea*, clade *Hymenophyllopsis* (Cyatheaceae).

#### MATERIALS AND METHODS

We examined ca. 150 herbarium and freshly collected specimens, given the difficulties in access to the region and collecting the species. These specimens were deposited in the following herbaria: INPA, MG, NY, RB, SP, UC, and US. Additionally, available images of herbarium specimens were also analyzed through the web (CR, F, GH, K, and MO). Two expeditions were carried out during 2016 to collect material for morphological and molecular studies. One of them explored the Tepui Roraima Mount, located in the Mount Roraima National Park, Roraima State, Brazil and the other at the Serra do Aracá Tepui, in the Serra do Aracá State Park, Amazonas State, Brazil. In total, 23 specimens were collected in these expeditions and deposited in the SP Herbarium (Instituto de Botânica) and the MG Herbarium (Museu Paraense Emílio Goeldi).

Spores of all species were analyzed using scanning electron microscopy (SEM) and their morphological characterization followed the terminology of Tryon and Lugardon (1991). The measurements of the spore size were made from the SEM photographs.

The distribution maps were compiled using QGIS software (QGIS Development Team, 2017). For materials with no geographical coordinates listed on the labels, we used the general coordinates of the tepuis, reported in Huber

(1995a, b) and at <http://www.dices.net/>. These estimated coordinates were cited between square brackets along the studied specimens.

Two indices are presented at the end of the taxonomic treatment: one of accepted names and one of collectors, which was made from all studied specimens. Numbers in parentheses in either index indicates the species number in the taxonomic treatment and the collectors' numbers in bold refer to the nomenclatural types.

## RESULTS AND DISCUSSION

**HABITAT.**—*Hymenophyllopsis* species are found in vegetation characterized by herbaceous-shrubby forest patches formed along the watercourses between rocky outcrops and cliffs. Pioneer communities grow on rocks and aquatic vegetation is also present (Huber, 1988, 1995a, b). This broad spectrum of habitats extends from the lower slopes, which are usually forested, to the flat and rocky surfaces carved by the constant action of heavy rain and wind (Maguire, 1970; Rull, 2005). This vegetation is found between 500 and 3000 m elevation (Rull, 2005). Rainfall in the region ranges from 2000 to 3350 mm annually, while the average temperature does not exceed 10°C during the day and can be as cold as 2°C at night. The climate varies from moderate to extremely humid (Maguire, 1970; Huber, 1988, 1995a, b; Michelangeli, 2000; Rull, 2005; Fig. 1A–F).

**MORPHOLOGY.**—*Habit.*—The species are generally rupicolous, but some may be terrestrial (e.g., *C. asplenoides* (A. C. Sm.) Christenh., *C. ctenitoides* (Lellinger) Christenh., and *C. hymenophylloides* (L. D. Gómez) Christenh.). These species grow between, on, or under rocks. More frequently, they are found in the cracks of the rocks, with their rhizomes protected inside the crack, which makes their collection difficult (Fig. 1C–F).

**Rhizomes.**—The rhizomes are erect with radial symmetry (i.e., petioles and roots borne in all directions), but may vary from suberect to erect in a single species, as for example in *C. alsophiloides* S. Maciel & Lehnert (Fig. 2A) and *C. cylindrica* S. Maciel & Lehnert. Only one species (*C. hymenophylloides*, Fig. 2B) has a short-creeping rhizome with bilateral symmetry (i.e., petioles protruding upwards and roots downwards). This characteristic can be used to distinguish *C. hymenophylloides* from all other species in the group. The erect rhizomes may form a small trunk, ranging from 1.0 to 3.5 cm in diameter (including roots, petioles, and scales) as in *C. ctenitoides* (Fig. 2C) or thinner trunks, up to 0.5 cm in diameter as in *C. alsophiloides* (Fig. 2A).

The rhizomes are protected by an indument of scales (Fig. 3A–E). These scales vary from around 2 mm long to 10–25 mm long, and in most species are: lanceolate (Fig. 3A, B, E); concolorous (Fig. 3B, C, D), light brown, brown to ferruginous; plane or twisted; with a truncate base and thick-walled cells and margins that range from entire or with short setiform projections mainly in the apex of the scale. *C. cylindrica* and *C. lellingeriana* S. Maciel & J. Prado have bicolorous scales (Fig. 3A, E). Oval-lanceolate scales are found only in *C.*

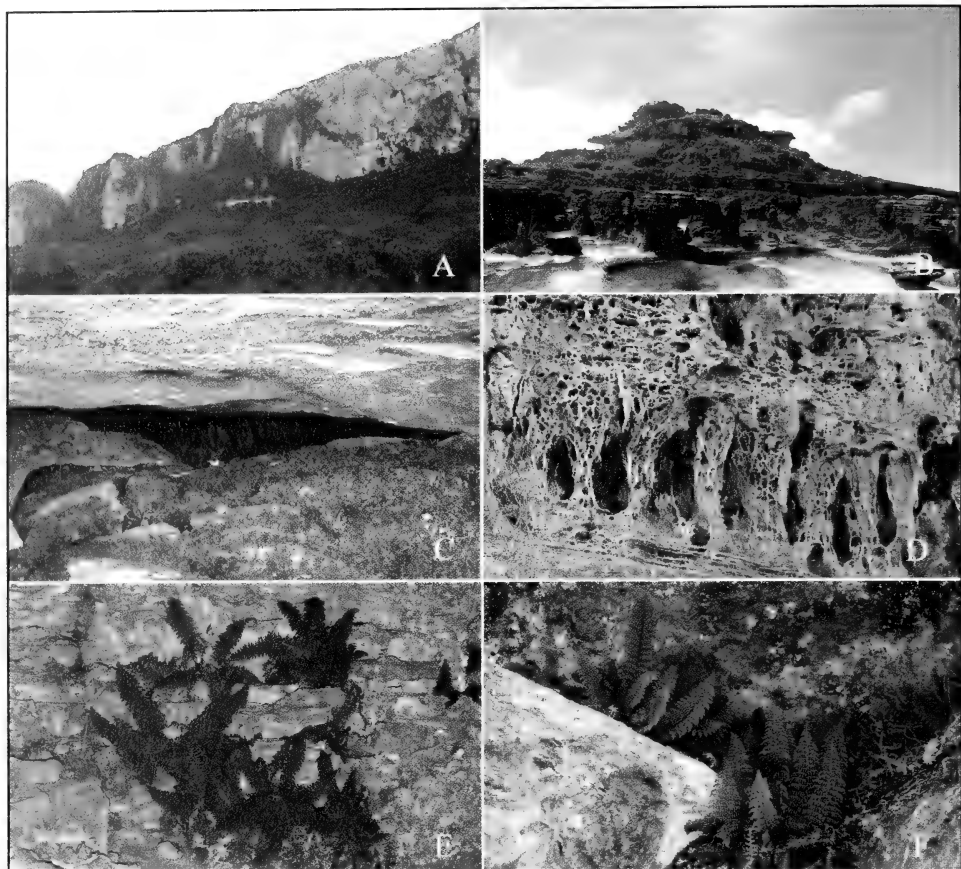


FIG. 1A–F. Habitats of the species of *Cyathea*, clade *Hymenophyllopsis* in the Mount Roraima National Park, Roraima State, Brazil (photos: A, C. Sebastião Maciel, 2016; B, D, E, F. Pedro Viana, 2016).

*hymenophylloides*, whereas linear scales (Fig. 3C) are present in *C. ctenitoides* and *C. trichomanoides* Christenh. Conspicuously twisted scales occur in *C. universitatis* (Fig. 3D). The apex of the scales also varies and may be acute and uniseriate as in *C. alsophiloides* (Fig. 3B), filiform and multiseriate as in *C. ctenitoides* (Fig. 3C) or short attenuate with only one cell, as in *C. cylindrica* (Fig. 3E).

*Leaves*.—The leaves vary from up to 7.5 cm to up to 40 cm (Fig. 4D, G) and from narrow (ca. 2.5 cm) to broad (ca. 7.5 cm; Fig. 4F, H). They are erect in almost all species, except in *C. trichomanoides* whose leaves are arched. In some species (e.g., *C. ctenitoides*) the leaves when dry may form a crown of fiddleheads at the apex of the rhizome (Fig. 2C).

*Laminae*.—The laminae provide good characters for identifying individual species and also for the recognition of two groups of species: one with pinnate lamina (Fig. 4A, C–G) and another with pinnatisect lamina (Fig. 4B, H). The

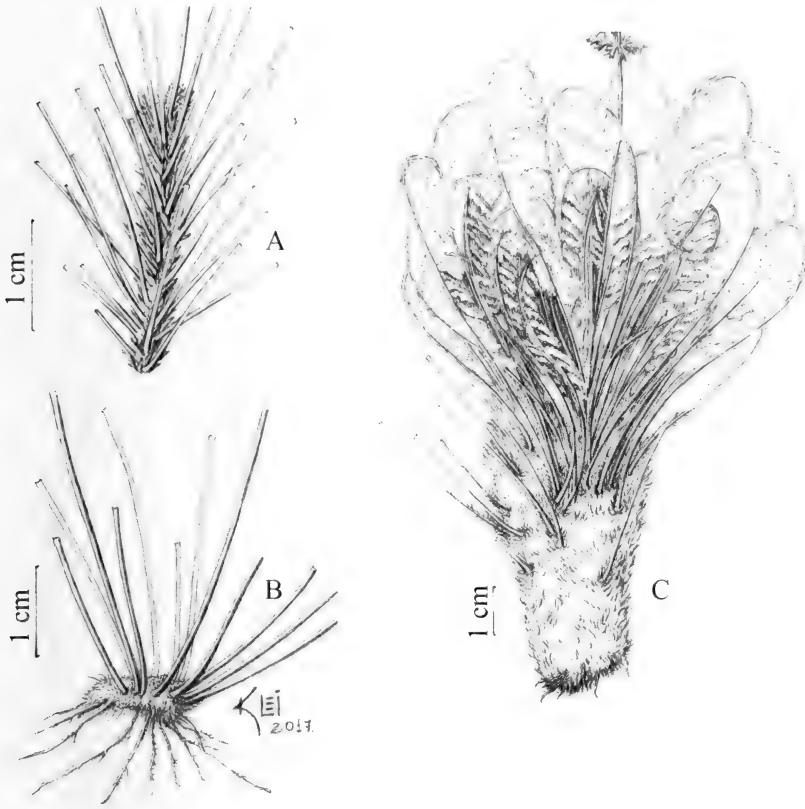


FIG. 2. Rhizomes of *Cyathea*, clade *Hymenophyllopsis*. A. Suberect, *C. alsophiloides* (Steyermark *et al.* 128825-A, holotype US). B. Short-creeping, *C. hymenophylloides* (Forzza *et al.* 6597, SP). C. Erect, *C. ctenitoides* (Steyermark & Wurdack 636, NY).

laminae are highly dissected, varying from 2- to 5- pinnate, the base varying from unreduced (Fig. 4A) to reduced (4B, E, F) or gradually reduced (4D, H). The laminae may be sparse (e.g., *C. alsophiloides*, Fig. 4A) or congested (e.g., *C. trichomanoides*, Fig. 4D).

*Petioles*.—Petioles vary from up to 5.0 cm (e.g., *C. asplenoides*, Fig. 5A) to up to 15 cm (e.g., *C. tatei* S. Maciel *et al.*, Fig. 5B). They are generally cylindrical (e.g., *C. minima* S. Maciel & J. Prado, Fig. 5C), but sometimes may be semi-cylindrical (e.g., *C. dejecta* (Baker) Christenh. and *C. tatei*, Fig. 5D, E), due to a groove on the adaxial face. Petiole diameter can range from 0.2 mm in *C. incognita* (Lellinger) Christenh. to 2.8 mm in *C. tatei*. The indument may also vary and be formed of scales or hairs (catenate and/or clavate) or the petioles may be glabrous.

*Rachises*.—The rachis morphology also varies and is useful for species identification. The rachis may be rounded (e.g., *C. incognita* and *C. hymenophylloides*, Fig. 5F, G), grooved (e.g., *C. indefinita* S. Maciel & J. Prado, Fig. 5H), or complanate (e.g., *C. asplenoides* and *C. alsophiloides*, Fig.

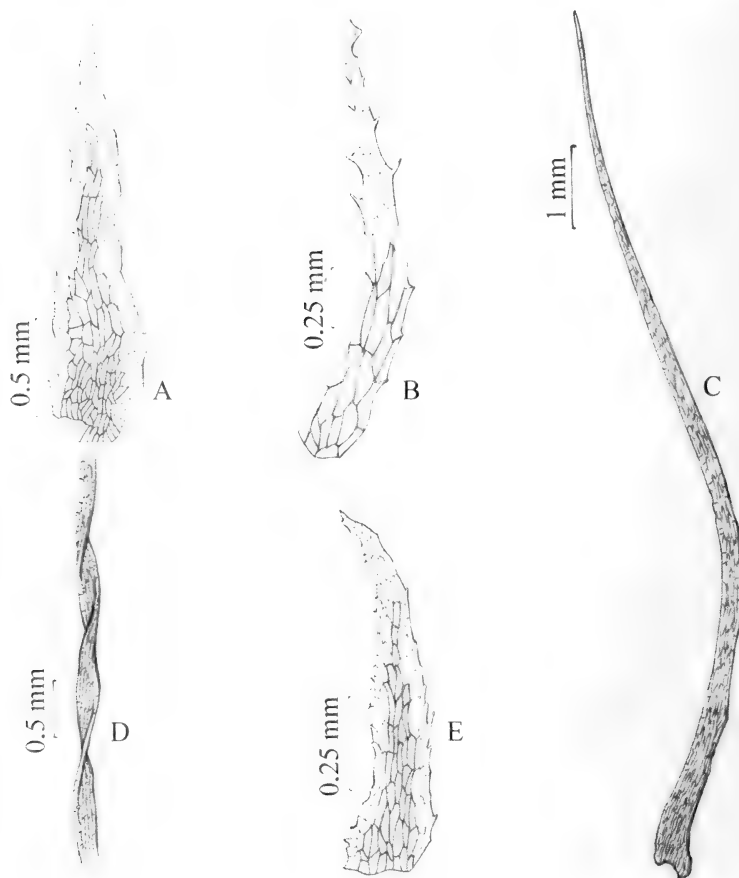


FIG. 3. Rhizome scales of *Cyathea*, clade *Hymenophyllopsis*. A. Lanceolate bicolorous scale (*C. lellingeriana*; Steyermark et al. 109201, holotype US). B. Scale with attenuate and uniseriate apex (*C. alsophiloides*; Steyermark et al. 128825-A, holotype US). C. Long, linear scale with filiform and multiseriate apex (*C. ctenitoides*; Steyermark & Wurdack 636, NY). D. Detail of a twisted scale (*C. universitatis*; Vareschi & Foldats 4938, isotype US). E. Bicolorous scale with short-attenuate apex (*C. cylindrica*; Liesner 17989, holotype US).

5I, J), winged or not, and glabrous or with indument formed of scales and/or hairs (Fig. 6A–H).

*Pinnae*.—Pinnae may be congested (in *C. trichomanoides*) or sparse (in *C. universitatis* (Vareschi) Christenh.) and are usually alternate. The pinnae may be patent (e.g., *C. trichomanoides*, Fig. 7A), recurved (e.g., *C. dejecta*, Fig. 7B), or ascending (e.g., *C. pseudoctenitoides* S. Maciel & J. Prado, *C. alsophiloides*, *C. asplenoides*, Fig. 7C–E).

*Venation*.—The veins can be simple (e.g., *C. alsophiloides*, Fig. 7D) or furcate (e.g., *C. ctenitoides*, Fig. 7H).

*Sori*.—Sori are usually abundant, occurring along the entire length of the pinna (e.g., *C. pseudoctenitoides*, Fig. 7C) or only at the apex of the pinna (e.g.,

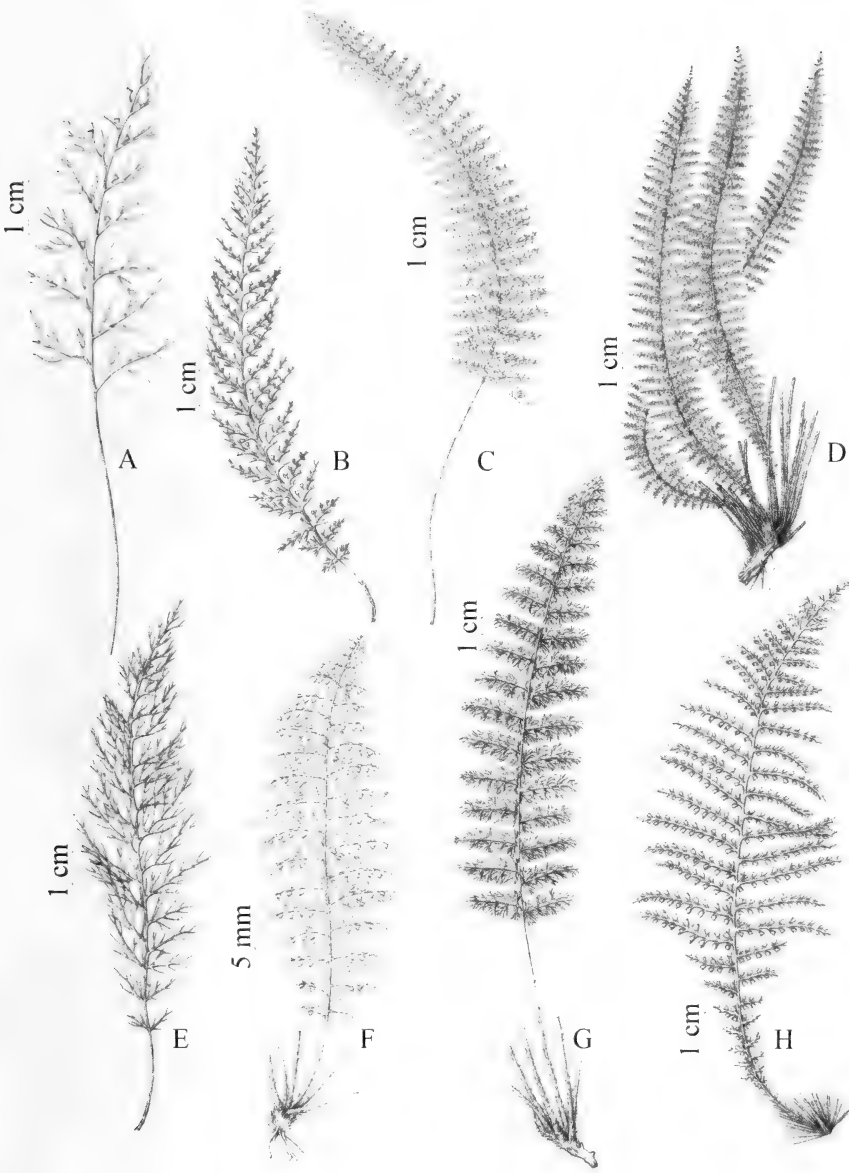


FIG. 4. Leaves and laminae of *Cyathea*, clade *Hymenophyllopsis*. A. Sparse lamina with base unreduced (*C. alsophiloides*; Steyermark et al. 128825-A, holotype US). B. Narrow lamina (*C. asplenoides*; Maguire et al. 46838, NY). C. Lamina with unreduced base (*C. lellingeriana*; Steyermark et al. 109201, isotype NY). D. Congested lamina (*C. trichomanoides*; Maguire et al. 42250, holotype US). E. Lamina with reduced base (*C. tepuiana*; Steyermark 75644, isotype US). F. Lamina with reduced base (*C. minima*; Boom et al. 6014, holotype NY). G. Pinnate lamina (*C. tatei*; Tate 445, holotype NY). H. Lamina gradually reduced (*C. universitatis*; Vareschi & Foldats 4938, isotype US).



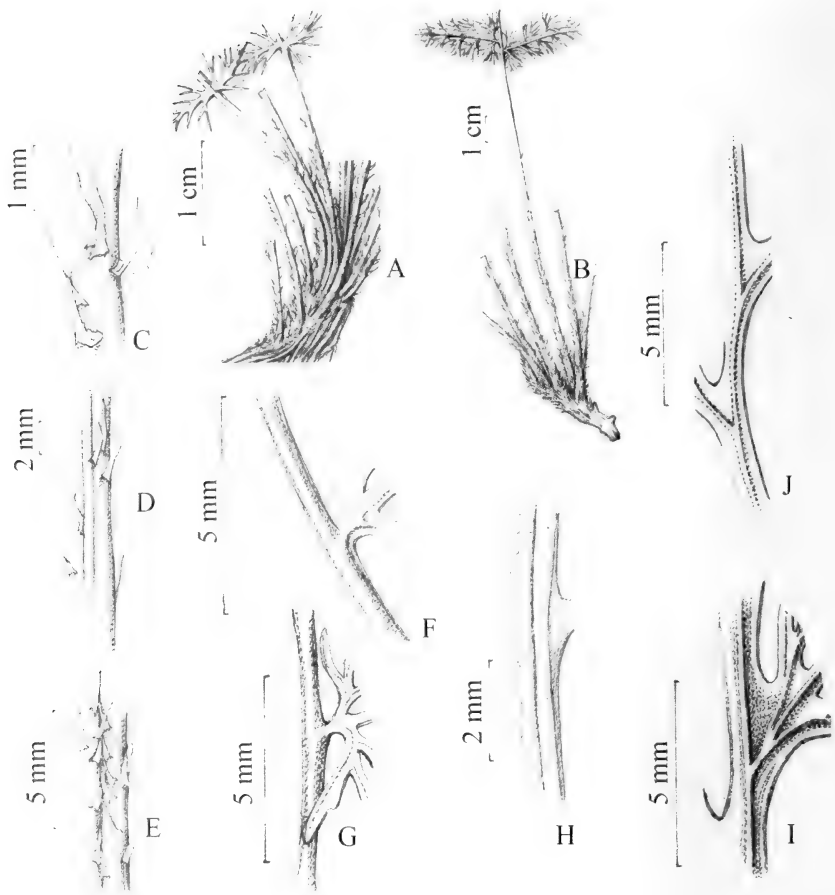


FIG. 5. Petioles and rachises of *Cyathea*, clade *Hymenophyllopsis*. A. Petiole of *C. asplenoides*; (Maguire et al. 46838, NY). B. Petiole of *C. tatei* (Tate 445, holotype NY). C. Cylindrical petiole (*C. minima*; Boom et al. 6014, holotype NY). D. Semi-cylindrical petiole (*C. dejecta*; Maciel & Viana 1860, SP). E. Semi-cylindrical petiole (*C. tatei*; Tate 445, holotype NY). F. Abaxial rachis surface of *C. incognita* (Steysmark 98014, holotype US). G. Adaxial rachis surface of *C. hymenophylloides* (Forzza et al. 6597, SP). H. Adaxial rachis surface of *C. indefinita* (Steysmark et al. 112515, holotype NY). I. Adaxial rachis surface of *C. asplenoides* (Maguire et al. 46838, NY). J. Abaxial rachis surface of *C. alsophiloides* (Steysmark et al. 128825-A, holotype US).

*C. dejecta*, Fig. 7B). The sori also vary from prominent in the margin of the lamina/segments (Fig. 7F, I, J) or immersed in the laminar tissue (Fig. 7G, H). There are no paraphyses in this group of *Cyathea*.

*Indusia*.—The indusia add two useful characteristics for distinguishing species. They can be bivalvate (e.g., *C. lellingeriana* and *C. tepuiana* Christenh., Fig. 7G, I) or cyatheoid (Fig. 7F, H, J, K) and their margins can be entire (e.g., *C. tepuiana*, Fig. 7I), sinuous, denticulate-lobed (e.g., *C. pseudoctenitoides*, Fig. 7K), fimbriate (e.g., *C. lellingeriana*, Fig. 7G) or deeply lacerate (e.g., *C. asplenoides*).

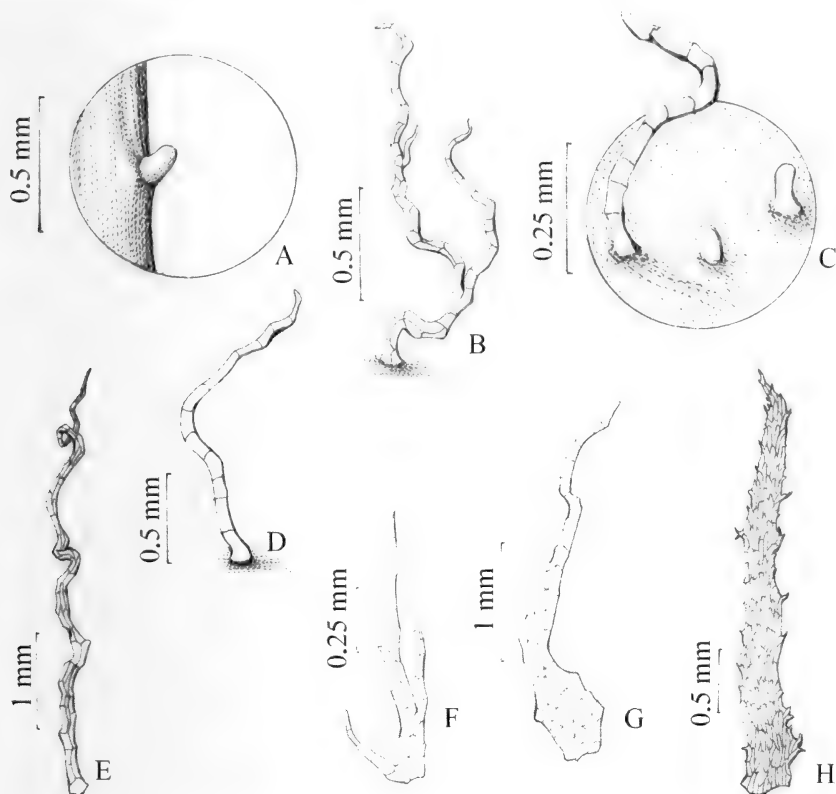


FIG. 6. Indument from rachises of *Cyathea*, clade *Hymenophyllopsis*. A. Clavate hair of *C. lellingeriana* (Steysmark et al. 109201, holotype US). B. Arachnoid scale of *C. ctenitoides* (Maciel & Viana 1852, SP). C. Catenate and clavate hairs of *C. cylindrica* (Liesner 17989, holotype US). D. Catenate hair of *C. pseudoctenitoides* (Steysmark et al. 126091, holotype US). E. Linear scale of *C. universitatis* (Vareschi & Foldats 4938, isotype US). F. Arachnoid scale of *C. tatei* (Tate 445, holotype NY). G. Bullate scale of *C. indefinita* (Steysmark et al. 112515, holotype NY). H. Lanceolate scale of *C. pseudoctenitoides* (Steysmark et al. 126091, holotype US).

**Sporangia.**—The sporangia are globose, sub-sessile, with an oblique annulus not interrupted by the pedicel of the sporangium. Each sporangium may form 32 spores per sporangium (*C. alsophiloides*, *C. asplenioides*, *C. cylindrica*, *C. incognita*, *C. tepuiana*, *C. trichomanoides*, and *C. universitatis*) or 64 (*C. ctenitoides*, *C. dejecta*, *C. hymenophylloides*, *C. indefinita*, *C. lellingeriana*, *C. minima*, *C. pseudoctenitoides*, and *C. tatei*; White and Turner, 2017 and in the present work).

**Spores.**—The spores are similar to the other *Cyathea* groups (Tryon and Lugardon, 1991) and are tetrahedral-globose and trilete without chlorophyll (Fig. 8A–F). The ornamentation varies from verrucate (Fig. 8A–C) to rugate (Fig. 8D–F) and they range in size from 40.0 to 74.0  $\mu\text{m}$  in diameter (Tryon and Lugardon, 1991 and in the present work). We observed a difference in the spore size associated with the number of spores per sporangium: species that

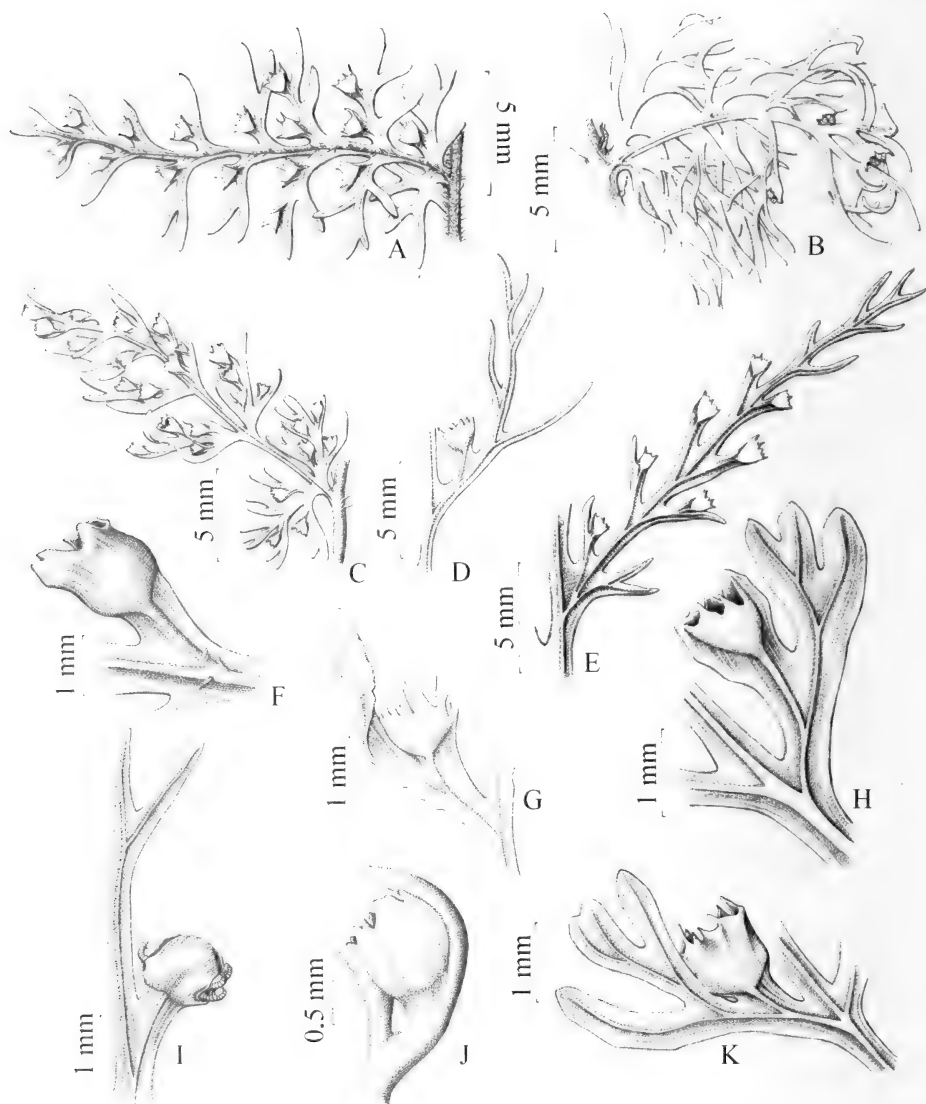


FIG. 7. Pinnae, venation, sori, and indusia of *Cyathea*, clade *Hymenophyllopsis*. A. Patent pinna of *C. trichomanoides* (Maguire et al. 42250, holotype US). B. Recurved pinna of *C. dejecta* (Huber 9515, NY). C. Sori of *C. pseudoctenitoides* (Steysmark et al. 126091, holotype US). D. Ascending pinna of *C. alsophiloides* (Steysmark et al. 128825-A, holotype US). E. Simple and furcated veins of *C. asplenoides* (Maguire et al. 46838, NY). F. Cyatheoid indusium of *C. universitatis* (Vareschi & Foldats 4938, isotype US). G. Vein and bivalvate indusium of *C. lellingeriana* (Steysmark et al. 109201, holotype US). H. Veins and cyatheoid indusium of *C. ctenitoides* (Steysmark & Wurdack 636, NY). I. Veins and bivalvate indusium of *C. tepuiana* (Steysmark 75644, isotype US). J. Cyatheoid indusium of *C. cylindrica* (Liesner 17989, holotype US). K. Veins and cyatheoid indusium of *C. pseudoctenitoides* (Steysmark et al. 126091, holotype US).

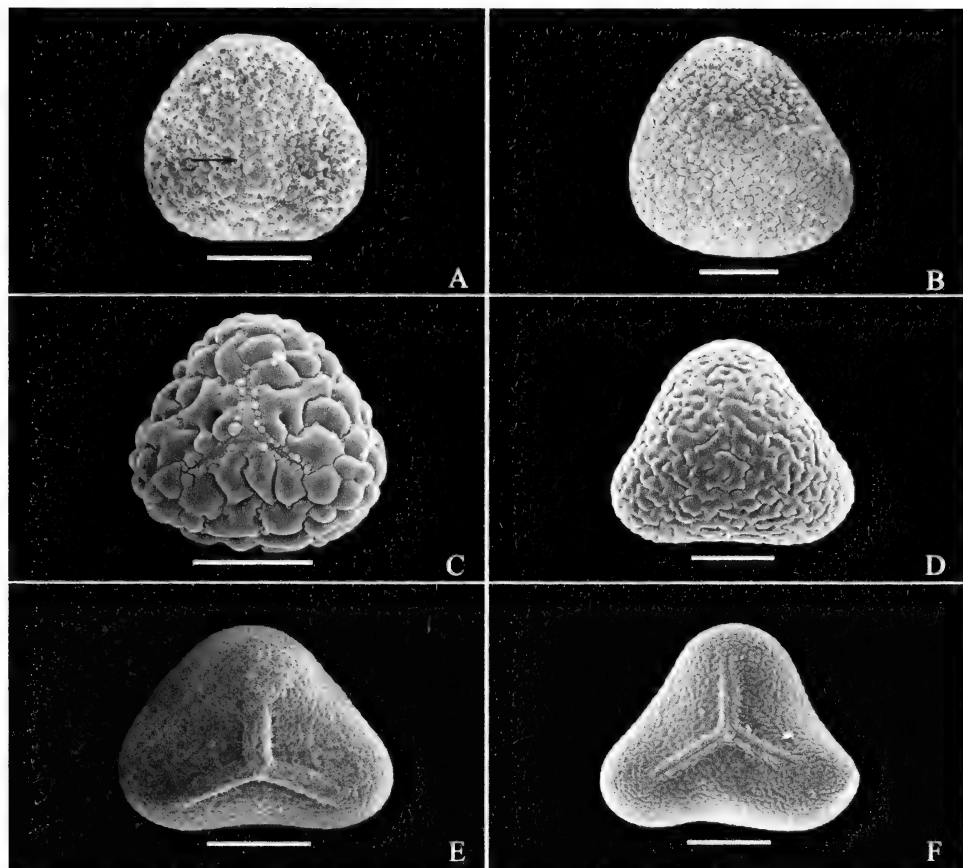


FIG. 8. Spores of *Cyathea*, clade *Hymenophyllopsis*. A. Proximal view, arrow indicating the aperture in *C. hymenophylloides* (Prance et al. 29149, NY). B. Distal view of *C. asplenoides* (Maguire & Politi 27764, NY). C. Proximal view of *C. ctenitoides* (Maciel & Viana 1852, SP). D. Distal view of *C. tepuiana* (Liesner 25302, NY). E. Proximal view of *C. indefinita* (Maciel & Viana 1856, SP). F. Proximal view of *C. minima* (Maciel & Viana 1874, SP). Scale bars = 20  $\mu\text{m}$ .

produce 32 spores/sporangium have bigger spores (56–74  $\mu\text{m}$  in diameter) than the species that produce 64 spores/sporangium (40–54  $\mu\text{m}$  in diameter). White and Turner (2017) obtained similar results for the group. Some species, such as *C. minima* and *C. dejecta*, with 64 spores/sporangium, have somewhat large spores (55–63  $\mu\text{m}$  in diameter) similar to some species with 32 spores/sporangium. The opposite is occasionally observed in *C. cylindrica*, *C. trichomanoides*, and *C. universitatis* that have 32 spores/sporangium; the spores have ca. 52  $\mu\text{m}$  in diameter.

**GEOGRAPHIC DISTRIBUTION.**—*Hymenophyllopsis* is endemic to the tepuis of the Guiana Shield (Fig. 9). The species occur mainly in the Venezuelan territory (Steyermark, 1986) and some of them have their areas of occurrence shared by the countries in which the Shield of the Guianas is inserted.

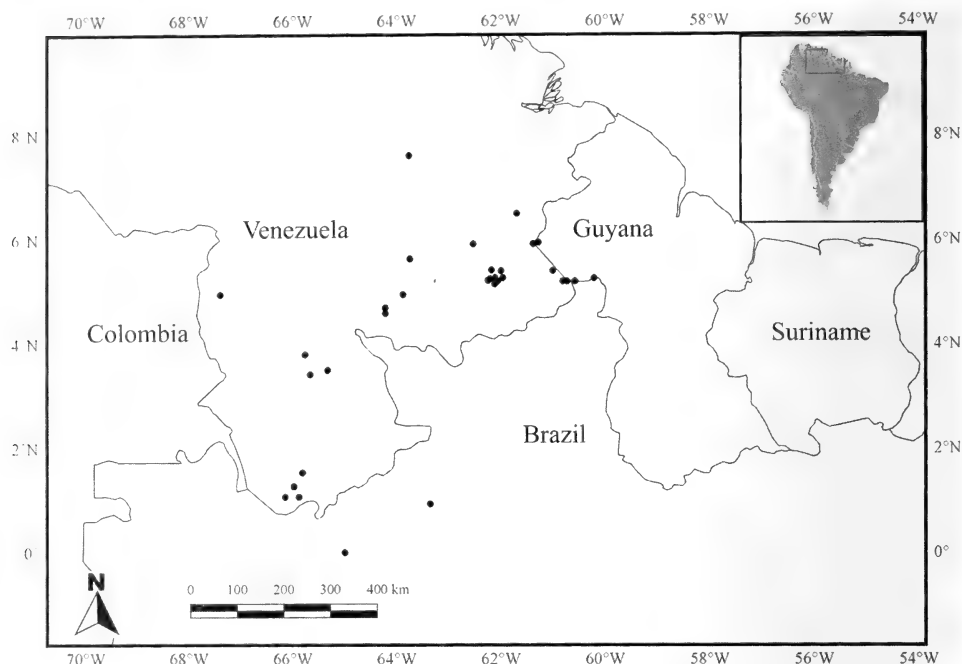


FIG. 9. Geographic distribution of *Cyathea*, clade *Hymenophyllopsis*.

The species are distributed in almost all the tepuis, but some are restricted to some massifs. For example, *C. universitatis* is limited to the Acopán-tepui of the Massif Chimantá and Auyán-tepui and *C. incognita* only occurs in the tepuis Agparamán-tepui of the Chimantá Massif and Meseta del Jáua. The richest place for *Hymenophyllopsis* is Mount Roraima (which includes portions of Brazil, Venezuela, and Guyana)—in this Tepui occur six of the 15 recognized species.

As pointed out by Moran (2008), there is a gap of studies in some of the most species-rich regions of the globe. The Brazilian tepui region is included in this list of interesting places and our data corroborate it, since the diversity reported here for the *Hymenophyllopsis* clade is 47% higher than the previous studies showed (8 species in Lellinger (1984) increased to 15 spp. here).

#### TAXONOMIC TREATMENT

*Cyathea* Sm., Mém. Acad. Roy. Sci. (Turin) 5: 416. 1793. TYPE.—*Polypodium arboreum* L. ( $\equiv$  *Cyathea arborea* (L.) Sm.).

= *Trichipteris* C. Presl, Delic. Prag. 1: 172. 1822. TYPE.—*Trichipteris excelsa* C. Presl.

= *Cnemidaria* C. Presl, Tent Pterid.: 56, tab. 1(16–18). 1836. TYPE.—*Cnemidaria speciosa* C. Presl.

= *Hymenophyllopsis* K. I. Goebel, Flora 124(1): 3, fig. 21. 1929  $\equiv$  *Cyathea* subg. *Hymenophyllopsis* (K. I. Goebel) Christenh., Phytotaxa 1: 38. 2009.  
 TYPE.—*Hymenophyllopsis dejecta* K. I. Goebel.

*Cyathea* is a monophyletic genus, with ca. 265 species widely distributed in the tropics and subtropics (PPG I, 2016). It is characterized by the presence of scales on the rhizome and base of the petioles, sporangia with an oblique annulus in relation to the pedicel of the sporangium, and trilete, tetrahedral-globose spores.

Most species in the genus are arborescent and terrestrial. However, some representatives are herbaceous and/or rupicolous, such as the species of the clade *Hymenophyllopsis*.

In the *Hymenophyllopsis* group, 15 species are recognized (Figs. 10–25), of which four are newly described here.

#### KEY TO THE SPECIES OF *CYATHEA*, CLADE *HYMENOPHYLLOPSIS*

1. Rhizomes short-creeping (with bilateral symmetry) . . . . . *C. hymenophylloides* (Fig. 17A–D)
1. Rhizomes erect to suberect (with radial symmetry)
  2. Laminae pinnatisect (2–3-pinnatisect)
    3. Rhizome scales 1.6–7.0 mm long; laminae narrow-lanceolate, 1.2–4.6 cm wide, congested, segments reduced toward the base . . . . . *C. asplenioides* (Fig. 10E–H)
    3. Rhizome scales 10.0–16.0 mm long; laminae broadly lanceolate, 2.0–7.5 cm wide, sparse, segments gradually reduced toward the base . . . *C. universitatis* (Fig. 25F–K)
  2. Laminae pinnate (1–5-pinnate-pinnatisect)
    4. Rhizome scales bicolorous
      5. Pinnae and pinnules cylindrical; ultimate segments with entire margins; rachises with two kinds of hairs (catenate and clavate) . . . . . *C. cylindrica* (Fig. 15A–E)
      5. Pinnae and pinnules with laminar tissue; ultimate segments with crenate to erose margins; rachises with one kind of hairs (clavate) . . . . . *C. lellingeriana* (Fig. 15F–J)
    4. Rhizome scales concolorous
      6. Rachises glabrous or with only sparse clavate hairs on both surfaces
        7. Petioles stout, 0.6–1.3 mm diam.; laminae congested. . . . . *C. tepuiana* (Fig. 24A–D)
        7. Petioles slender, 0.2–0.5 mm diam.; laminae sparse
          8. Rhizome scales with short sparse setiform projections toward the apex; laminar tissue reduced (0.1–0.2 mm wide of each side of the costule); sori prominent in the laminar tissue . . . . . *C. alsophiloides* (Fig. 10A–D)
          8. Rhizome scales with entire margins; laminar tissue broad (0.3–0.5 mm wide of each side of the costule); sori immersed in the laminar tissue . . . . . *C. incognita* (Fig. 17E–H)
      6. Rachises with scales and hairs (clavate or catenate) on both surfaces
        9. Rachises with dense indument of scales (one kind) and hairs (catenate and clavate), the scales and the catenate hairs hyaline . . . . . *C. trichomanoides* (Fig. 25A–E)
        9. Rachises with scales (one or two kinds) and hairs (catenate and clavate), the scales paleaceous, brown to reddish brown or ferrugineous, the hairs catenate brown to reddish brown

10. Rhizome scales  $\geq 10$  mm long (up to 25 mm), linear, ferrugineous . . . . . *C. ctenitoides* (Fig. 13A–E)
  10. Rhizome scales  $< 10$  mm long, narrow-lanceolate to broadly lanceolate, paleaceous, brown, light brown or reddish brown
    11. Pinnae patent; pinnae apex recurved
      12. Petioles semi-cylindrical; rachises with one kind of scales (lanceolate); sori generally prominent . . . . . *C. dejecta* (Fig. 16A–F)
      12. Petioles cylindrical; rachises with two kinds of scales (lanceolate and bullate); sori generally immersed in the laminar tissue . . . . . *C. minima* (Fig. 19H–M)
    11. Pinnae ascending or patent; pinnae apex not recurved
      13. Proximal pinnae gradually reduced . . . . . *C. pseudoctenitoides* (Fig. 13F–K)
      13. Proximal pinnae reduced or slightly reduced
        14. Proximal pinnae reduced; rachises with one kind of scales (bullate) *C. indefinita* (Fig. 19A–G)
        14. Proximal pinnae slightly reduced; rachises with two kinds of scales (lanceolate and arachnoid) . . . . . *C. tatei* (Fig. 16G–L)
1. *Cyathea alsophiloides* S. Maciel & Lehnert, Phytotaxa 329(2): 160, figs. 1A–D, 3. 2017. TYPE: VENEZUELA. **Bolívar**: Piar. Macizo del Chimantá, sección oriental del Chimantá-tepui, cabeceras del afluente derecho superior del Río Tirica (“Caño del Grillo”), 05°18’N, 62°03’W, 2450 m, 7–9 Feb 1983, J.A. Steyermark, O. Huber & V. Carreño 128825-A (holotype: US barcode US00785468!; isotype: VEN, not seen) (Figs. 10A–D, 11).

**Plants** rupicolous, rarely terrestrial. **Rhizomes** suberect to erect, 1.0–1.2 mm diam. (2.4–5.0 mm diam., including roots, petioles, and scales), scaly, surface of the rhizome visible, the scales  $1.0\text{--}2.2 \times 0.15\text{--}0.2$  mm, concolorous, brown to dark brown, lustrous, lanceolate, slightly contorted, bases truncate, cells of the scale body with thick walls, margins with short sparse setiform projections toward the apex, apices acute (uniseriate), 0.2–0.25 mm long, brown or reddish brown. **Leaves**  $5.6\text{--}11.6 \times 1.7\text{--}2.8$  cm, caespitose, erect; **petioles** slender, 0.3–0.4 mm diam., 1.8–4.3 cm long, dark brown to dark purple, cylindrical, proximal region with sparse scales similar to those of the rhizome, distally glabrous; **laminae**  $3.8\text{--}7.3 \times 1.7\text{--}2.8$  cm, 3-pinnate-pinnatisect, lanceolate, sparse, proximal pinnae unreduced or slightly reduced, distal ones reduced, proximal segments not overlapping the rachis and secondary rachis; **rachises** complanate on both surfaces, occasionally rounded, not winged, glabrous on both surfaces; **pinnae** ca.  $1.5 \times 0.7$  cm, lanceolate, sparse, 3–8 pairs, costae inconspicuous, alternate, ascending; **secondary rachises** inconspicuous, glabrous on both surfaces; **segments** entire, pinnatisect, costules inconspicuous, with one pair of lateral veins, veins alternate, simple, occasionally



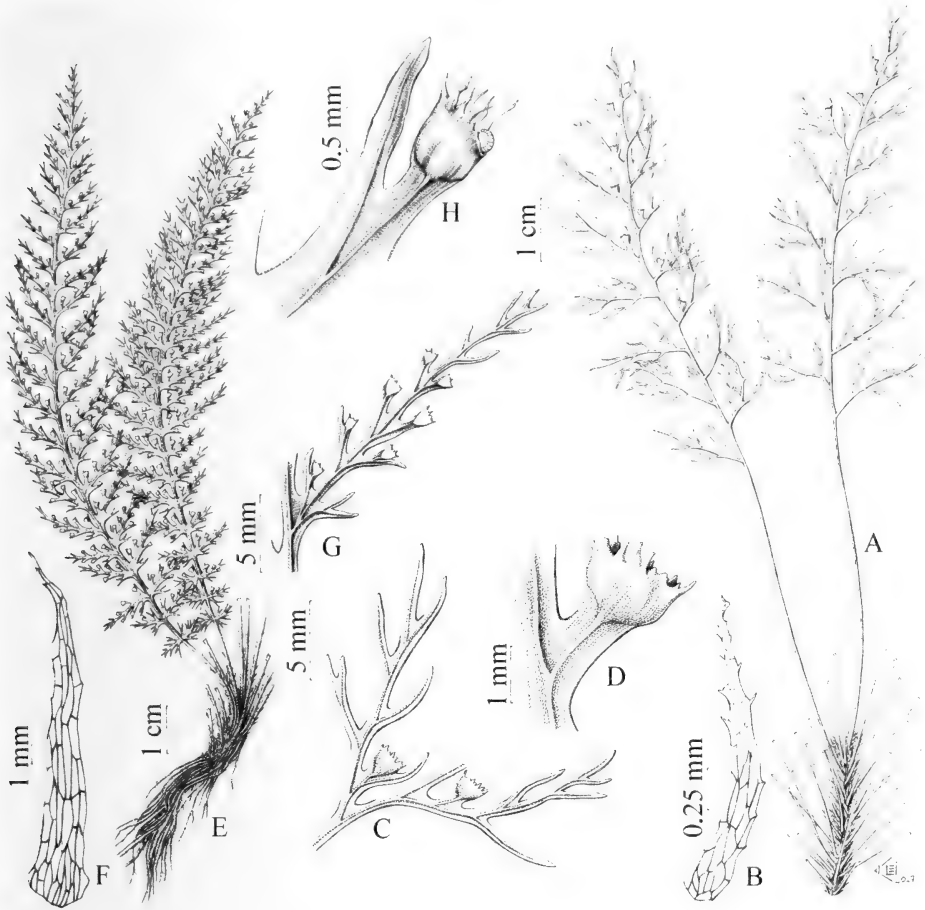


FIG. 10. A–D: *Cyathea alsophiloides*. A. Habit. B. Rhizome scale. C. Segment abaxially. D. Indusium. E–H: *C. asplenoides*. E. Habit. F. Rhizome scale. G. Segment adaxially. H. Indusium and margin of the lamina (A–D: Steyermark et al. 128825-A, holotype US; E, G–H: Maguire et al. 46838, NY; F: Tate 439, holotype NY).

furcated; **laminar tissue** reduced, 0.05–0.1 mm wide of each side of the secondary rachis, 0.1–0.2 mm wide of each side of the costule; **ultimate segments** with entire margins, apices acute, occasionally rounded; **sterile segments** 0.2–0.4 mm wide; **fertile segments** 0.4–0.7 mm wide. **Sori** 1–6 per pinna, prominent in the laminar tissue, usually borne on the acroscopic base of the basal segments, near rachis; **indusia** fragile, bivalvate, abaxial valve ca. 0.6 mm long, margin subentire to denticulate-lobed, adaxial valve ca. 0.8 mm long, margin subentire to sinuose; **spores** 32 per sporangium, yellowish, surface and aperture not seen.

*Distribution and ecology.*—*Cyathea alsophiloides* occurs only in Venezuela (Bolívar), in the Chimantá-tepui and Ptari-tepui; 2360–2450 m elevation. It

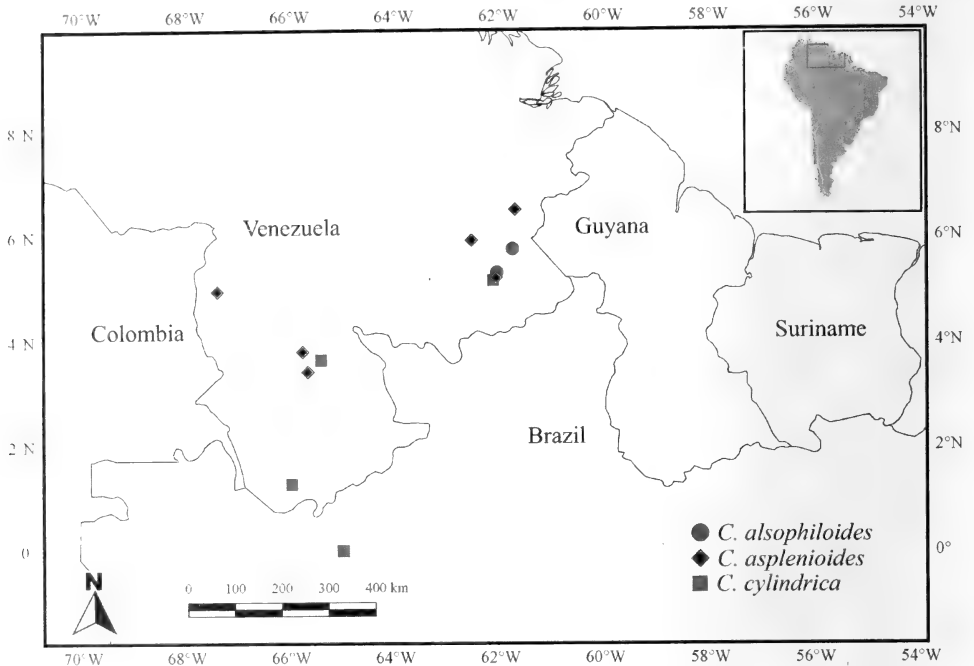


FIG. 11. Distribution of *C. alsophiloides*, *C. asplenioides*, and *C. cylindrica*.

grows in crevices of shaded rocks and under the edges of cliffs and small caves (Maciel *et al.*, 2017).

*Specimens examined*.—VENEZUELA. **Bolívar**: Cumbre del Ptari-tepui, al norte de la Misión de Santa Teresita de Kavanayén, 05°45'N, 61°45'W, 2360–2420 m, 23 Feb 1978, J.A. Steyermark *et al.* 115680 (US); Piar, Macizo del Chimantá, sección oriental del Chimantá-tepui, cabeceras del afluente derecho superior del Río Tirica (“Caño del Grillo”), 05°18'N, 62°03'W, 2450 m, 7–9 Feb 1983, J.A. Steyermark *et al.* 128825 (NY), 129012 (US).

*Cyathea alsophiloides* can be recognized by the sparse laminae that are proximally unreduced or slightly reduced (Fig. 10A). According to Maciel *et al.* (2017), the rhizome scales have short, sparse, setiform marginal projections toward the apex (Fig. 10B), and the rachises are glabrous on both surfaces (Fig. 10C).

2. *Cyathea asplenioides* (A. C. Sm.) Christenh., Phytotaxa 1: 39. 2009. *Hymenophyllopsis asplenioides* A. C. Sm., Bull. Torrey Bot. Club 58: 302, tab. 22. 1931. *Asplenium asplenioides* (A. C. Sm.) Pittier, Cat. Fl. Venez 1: 45. 1945, *nom. illeg.* TYPE: VENEZUELA. [Amazonas:] Summit of mount Duida, [03°25'N, 65°40'W], 5500–6000 ft [1676–1828 m], 26 Nov–16 Dec 1928, G.H.H. Tate 439 (holotype: NY barcode NY00144734!; isotype: US barcode US00065651!) (Figs. 10E–H, 11, 12A, B).

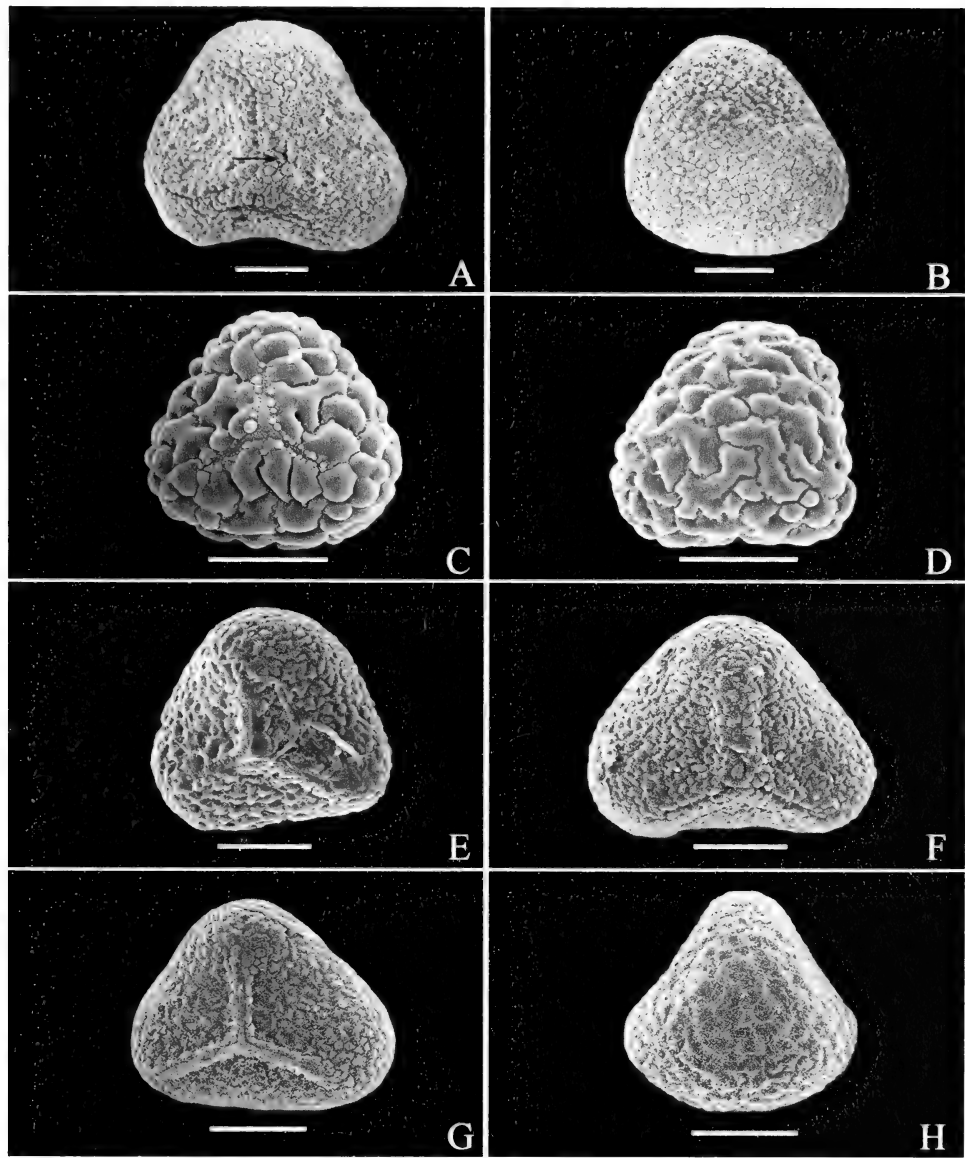


FIG. 12. Spores of *Cyathea*, clade *Hymenophyllopsis*. A–B: *C. asplenioides*. A. Proximal view, arrow indicating the aperture. B. Distal view (A–B: Maguire & Politi 27764, NY). C–D: *C. ctenitoides*. C. Proximal view. D. Distal view (C–D: Maciel & Viana 1852, SP). E: *C. cylindrica*, proximal view (E: Steyermark 103893, NY). F: *C. incognita*, proximal view (F: Steyermark & Wurdack 1141, NY). G–H: *C. dejecta*. G. Proximal view. H. Distal view (G–H: Maciel & Viana 1860, SP). Scale bars = 20  $\mu$ m.

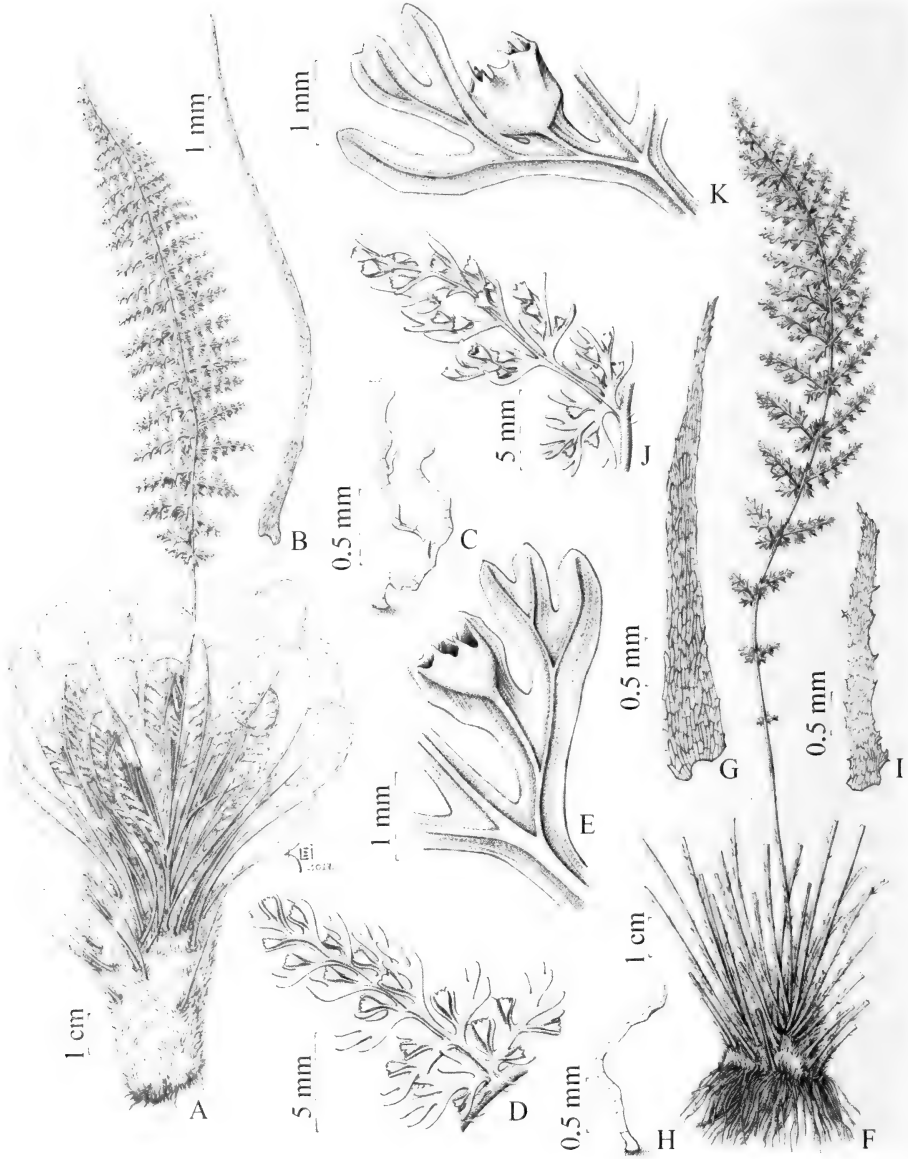


FIG. 13. A–E: *Cyathea ctenitoides*. A. Habit. B. Rhizome scale. C. Rachis scale. D. Pinna adaxially. E. Indusium and margin of the lamina. F–K: *C. pseudoctenitoides*. F. Habit. G. Rhizome scale. H. Hair from rachis. I. Rachis scale. J. Pinna adaxially. K. Indusium and margin of the lamina (A–B, D–E: Steyermark & Wurdack 636, NY; C: Maciel & Viana 1852, SP; F–K: Steyermark et al. 126091, holotype US).

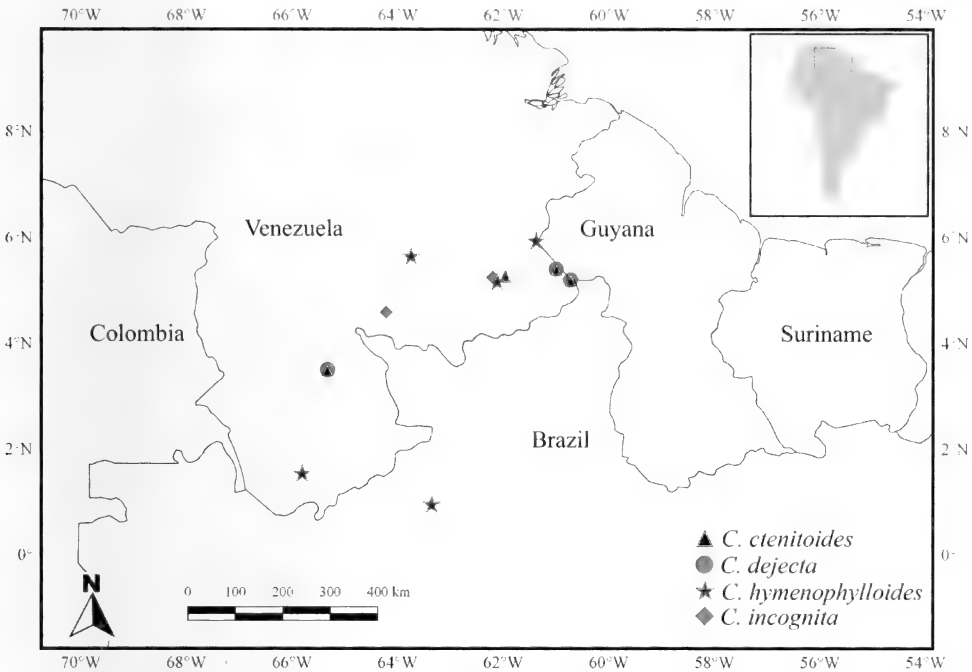


FIG. 14. Distribution of *C. ctenitoides*, *C. dejecta*, *C. hymenophylloides*, and *C. incognita*.

**Plants** rupicolous or terrestrial. **Rhizomes** erect, 0.8–2.5 mm diam. (2.7–12.5 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome visible, scales 1.6–7.0 × 0.2–0.3 mm, concolorous, light brown to brown, lustrous, lanceolate, contorted, bases truncate, occasionally rounded, cells of the scale body with thick walls, margins entire, seldom with few short setiform projections toward the apex, apices acute (uniseriate), 0.1–0.15 mm long, brown. **Leaves** 3.0–20.0 × 1.2–4.6 cm, caespitose, erect; **petioles** stout (0.5–)0.6–1.0 mm diam., 0.5–5.0(–8.0) cm long, dark brown to dark purple, cylindrical, not winged proximally, winged distally, the wings 0.05–0.1 mm wide, with scales similar to those of the rhizomes, shorter, sparse, rarely with clavate hairs, 0.1–0.2 cm long, brown to reddish brown; **laminae** 3.0–15.0 × 1.2–4.6 cm, 3-pinnatisect at base, 2-pinnatisect distally, narrow-lanceolate, congested, proximal and distal segments reduced, proximal segments usually not overlapping the rachis and costa; **rachises** abaxially slightly rounded, adaxially complanate, winged, the wings 0.1–0.5 mm wide, glabrous on both surfaces or occasionally with few scales and clavate hairs abaxially, similar to those of the petioles; **segments** 0.5–3.0 × 0.4–0.7 cm, lanceolate, sparse, (7–)10–30 pairs, costae inconspicuous, opposite, sometimes alternate, usually ascending; **costae** inconspicuous, usually glabrous on both surfaces or occasionally with few clavate hairs abaxially; **ultimate segments** entire, pinnatisect, costules inconspicuous, with one pair of lateral veins, veins alternate, simple or furcate, margins entire, sometimes sinuose, apices acute; **laminar tissue** broad, 0.2–0.5 mm wide on each side of the costa,

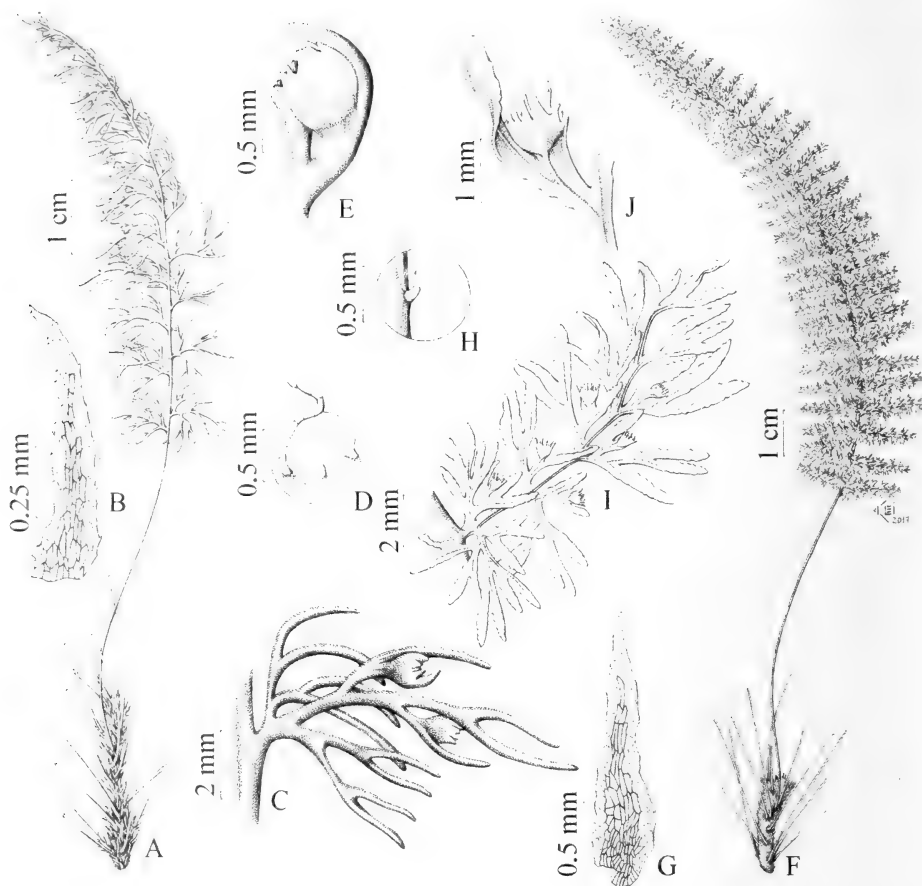


FIG. 15. A–E: *Cyathea cylindrica*. A. Habit. B. Rhizome scale. C. Pinna adaxially. D. Hairs from rachis. E. Indusium and segment. F–J: *C. tellingeriana*. F. Habit. G. Rhizome scale. H. Hair from rachis. I. Pinna abaxially. J. Indusium and margin of the lamina (A–E: Liesner 17989, holotype US; F: Steyermark et al. 109201, isotype NY; G–J: Steyermark et al. 109201, holotype US).

0.2–0.4 mm wide on each side of the costule; **sterile segments** 0.2–0.6 mm wide; **fertile segments** 0.4–1.2 mm wide. **Sori** 2–10 per segment, prominent in the laminar tissue, rarely immersed, borne at acroscopic and basiscopic bases of the proximal and distal segments, rarely at apex of the segments; **indusia** robust, bivalvate, valves adaxial and abaxial 0.4–1.5 mm long, margins deeply lacerate, fimbriate, sometimes denticulate-lobed; **spores** 32 per sporangium, 56–74  $\mu$ m in diam., orangish, surface finely verrucate and aperture inconspicuous.

*Distribution and ecology.*—It occurs only in Venezuela (Amazonas and Bolívar), in four tepuis of the Chimantá Massif (Acopán-tepui, Amurí-tepui, Chimantá-tepui, and Murú-tepui), Cerro Duida, Cerro Huachamacari, Cerro Sipapo, Auyán-tepui, and Ptarí-tepui. *Cyathea asplenioides* grows preferentially near streams, in very humid cliffs, with running water, and also in cracks of rocks; 850–2300 m elevation.

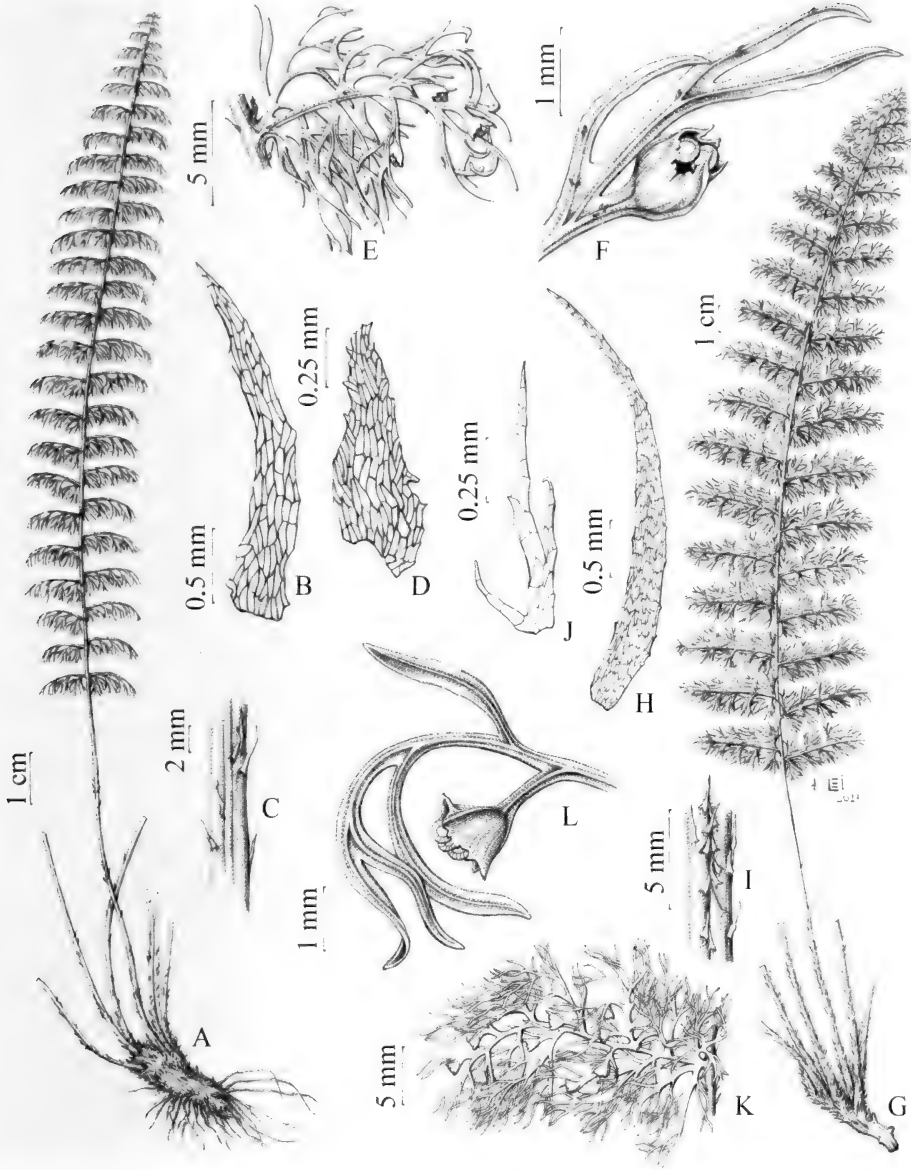


FIG. 16. A–F: *Cyathea dejecta*. A. Habit. B. Rhizome scale. C. Petiole adaxially. D. Rachis scale. E. Pinna abaxially. F. Indusium and margin of the lamina. G–L: *C. tatei*. G. Habit. H. Rhizome scale. I. Petiole adaxially. J. Rachis scale. K. Pinna abaxially. L. Indusium and margin of the lamina (A, E–F: Huber 9515, NY; B–C: Maciel & Viana 1860, SP; D: Maciel & Viana 1876, SP; G–L: Tate 445, holotype NY).

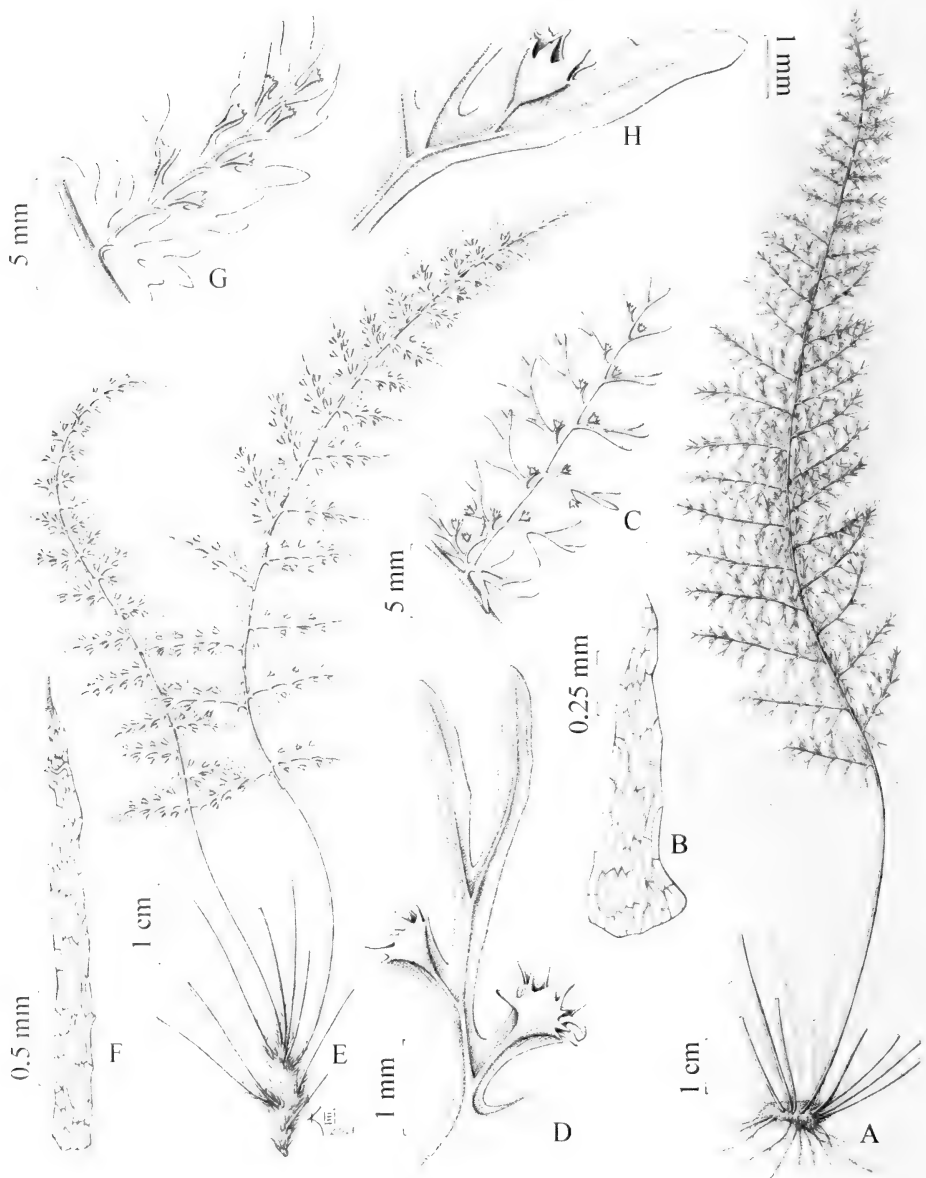


FIG. 17. A–D: *Cyathea hymenophylloides*. A. Habit. B. Rhizome scale. C. Pinna abaxially. D. Indusium and margin of the lamina. E–H: *C. incognita*. E. Habit. F. Rhizome scale. G. Pinna abaxially. H. Indusium and margin of the lamina (A, C–D: Forzza et al. 6597, SP; B: Steyermark et al. 92584, isotype NY; E–H: Steyermark 98014, holotype US).



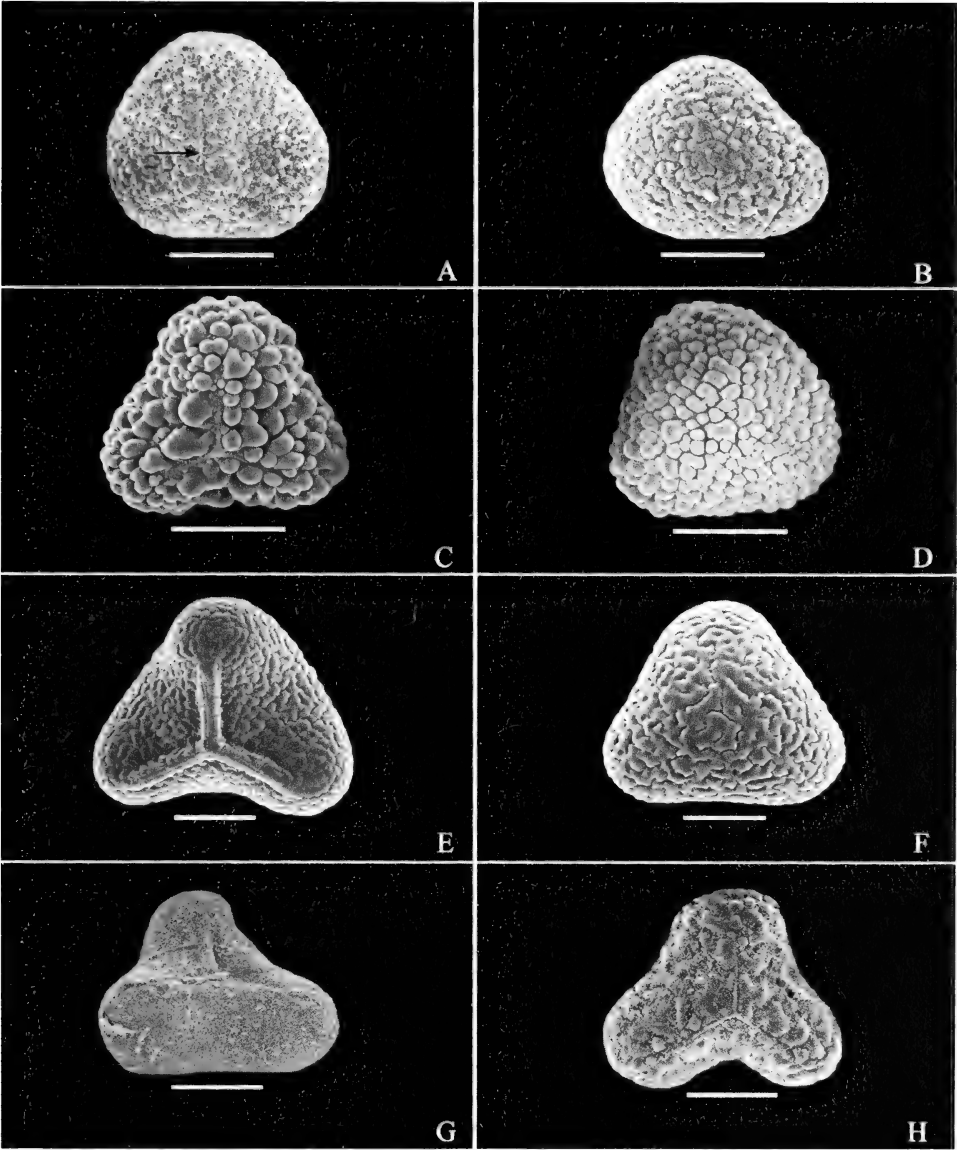


FIG. 18. Spores of *Cyathea*, clade *Hymenophyllopsis*. A–B. *C. hymenophylloides*. A. Proximal view, arrow indicating the aperture. B. Distal view (A–B: *Prance et al.* 29149, NY). C–D: *C. lellingeriana*. C. Proximal view. D. Distal view (C–D: *Steiermark & Nilsson* 25, NY). E–F: *C. tepuiana*. E. Proximal view. F. Distal view (E–F: *Liesner* 25302, NY). G: *C. trichomanoides*. Proximal view (G: *Liesner & Carnevali* 22424, NY). H: *C. universitatis*, Proximal view (H: *Steiermark* 94041, NY). Scale bars = 20  $\mu$ m.

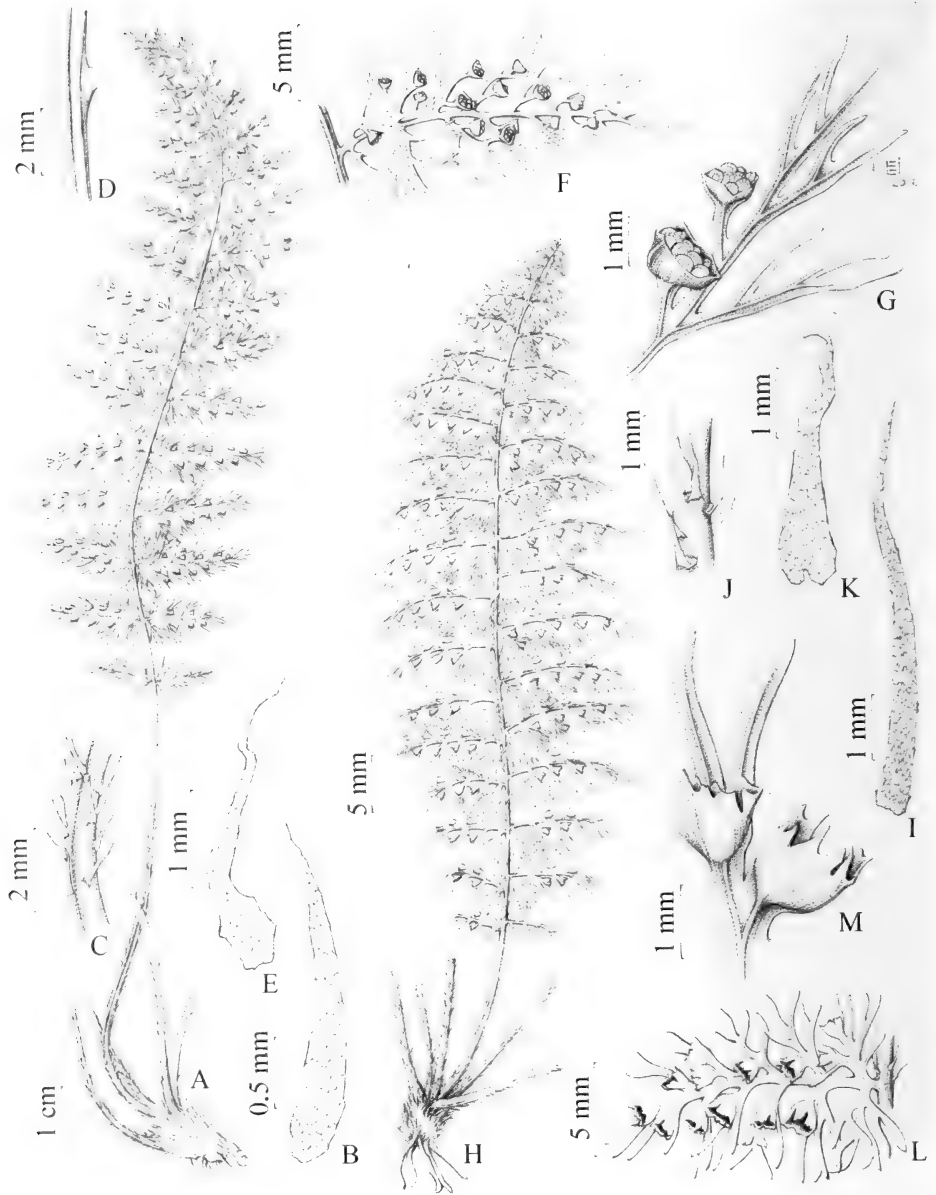


FIG. 19. A–G: *Cyathea indefinita*. A. Habit. B. Rhizome scale. C. Petiole adaxially. D. Rachis adaxially. E. Rachis scale. F. Pinna adaxially. G. Indusium and margin of the lamina. H–M: *C. minima*. H. Habit. I. Rhizome scale. J. Petiole adaxially. K. Rachis scale. L. Pinna adaxially. M. Indusium and margin of the lamina (A–G: Steyermark *et al.* 112515, holotype NY; H–M: Boom *et al.* 6014, holotype NY).

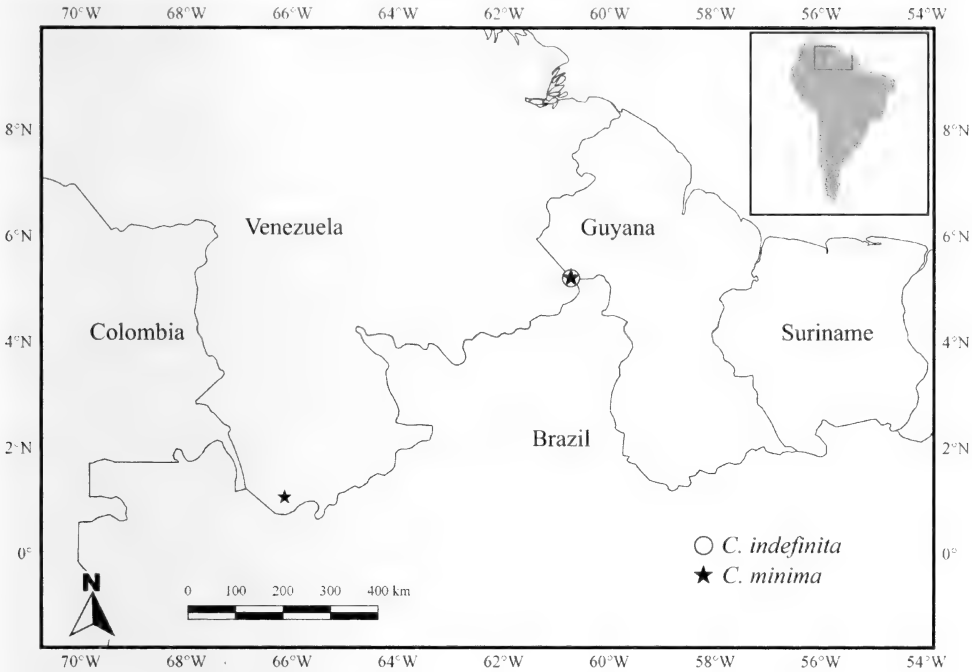


FIG. 20. Distribution of *C. indefinita* and *C. minima*.

*Specimens examined*.—VENEZUELA. **Amazonas**: Summit of cerro Duida, along valley forest between central camp and Brocchinia Hills, [03°25'N, 65°40'W], 1675 m, 31 Aug 1944, *J.A. Steyermark* 58100 (NY); Cerro Sipapo (Paráque), [04°57'N, 67°24'W], 1400 m, 17 Dec 1948, *B. Maguire & L. Politi* 27764 (NY); Cerro Sipapo (Paráque), [04°57'N, 67°24'W], 10 Jan 1949, *B. Maguire & L. Politi* 28279 (NY); Cerro Huachamacari, Río Cunucunuma, [03°48'N, 65°46'W], 5 Dec 1950, *B. Maguire et al.* 29889 (NY). **Bolívar**: Alto Río Cuyuni, Río Uiri-yuk, [06°30'N, 61°42'W], 850 m, 20–21 Aug 1962, *B. Maguire et al.* 46838 (NY); Murú-tepui, north of Camp 8, northwest slopes of Churitepui (Murú-tepui), [05°16'N, 61°58'W], 2050 m, 01 Feb 1953, *J.J. Wurdack* 34287 (NY); Auyán-tepui, en la parte superior, [05°55'N, 62°32'W], 2300 m, 20 Apr 1956, *V. Vareschi & E. Foldats* 28279 (NY); Chimantá massif, vicinity of camp 4, southwestern edge of Apácaratepui, [05°16'N, 62°07'W], 1800–2000 m, 14 Apr 1953, *J.A. Steyermark* 74990 (NY); Chimantá Massif, Amurí-tepui, base of southwest-facing escarpment, [05°08'N, 62°07'W], 1365 m, 10 Mar 1955, *J.A. Steyermark & J.J. Wurdack* 1360 (NY); Macizo del Chimantá, sector SSE, altiplanicie sur-oriental del Acopán-tepui, cabeceras del Río Arauac, 05°11'N, 62°00'W, 1920 m, 14–16 Feb 1984, *J.L. Luteyn et al.* 9507 (NY).

*Cyathea asplenioides* has narrow-lanceolate laminae, 3.0–15.0 × 1.2–4.6 cm, congested, with many pairs of segments (10–30), usually ascending (Fig. 10E). The costae are glabrous on both surfaces, the sori prominent in the laminar tissue, usually occurring on the acroscopic and basiscopic bases of the

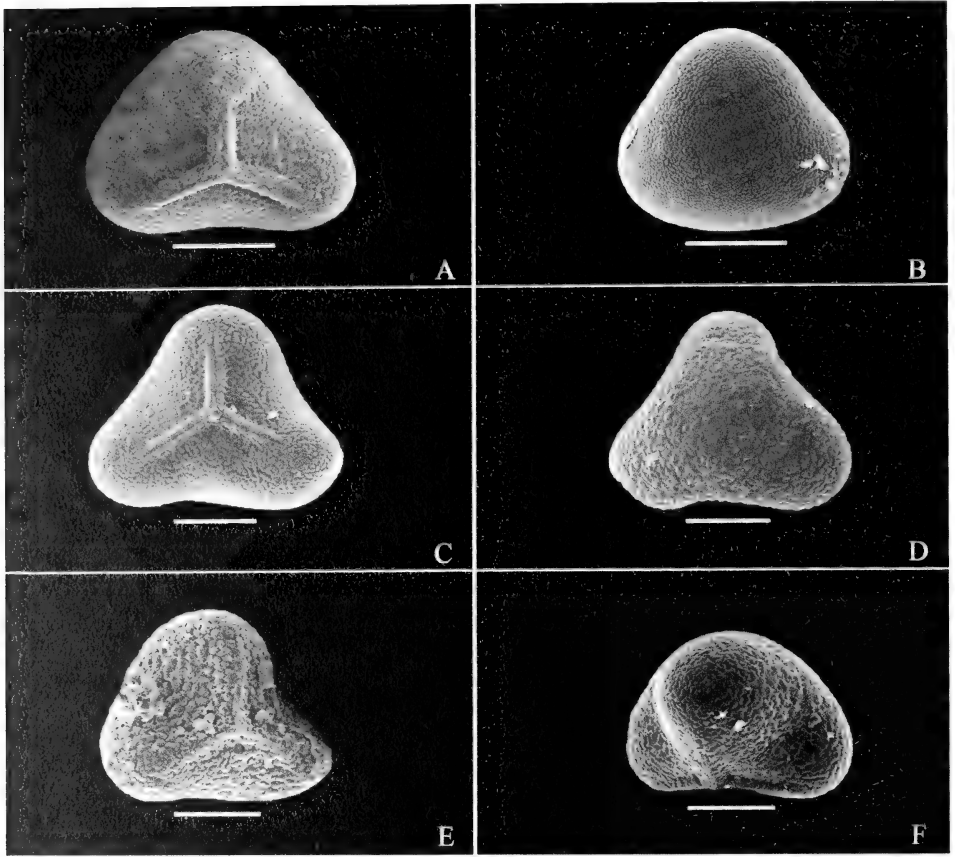


FIG. 21. Spores of *Cyathea*, clade *Hymenophyllopsis*. A–B: *C. indefinita*. A. Proximal view. B. Distal view (A–B: Maciel & Viana 1856, SP). C–D: *C. minima*. C. Proximal view. D. Distal view (C–D: Maciel & Viana 1874, SP). E: *C. pseudoctenitoides*, Proximal view (E: Steyermark 126091 et al., NY). F: *C. tatei*, Proximal view (F: Maciel & Viana 1870, SP). Scale bars = 20  $\mu$ m.

proximal and distal segments (Fig. 10G), with sori robust, bivalvate, and margins generally deeply lacerate (Fig. 10H).

The morphology of *C. asplenioides* varies according to the place where the plants grow. Typical plants have short petioles (0.5–5.0 cm long) and generally grow in wet places or with running water on rocks (Maguire et al. 29889, NY), whereas the specimens growing in rock-shaded cracks have petioles that are 5.0–8.0 cm long (Steyermark 74876, US; Holst et al. 2901, US). Terrestrial plants have greatly reduced laminar tissue (ca. 0.3 mm wide on each side of the costa, ca 0.2 mm wide on each side of the costule) and fewer pairs of segments, 7–13 pairs (Huber & Dezzio 8662, NY; Steyermark et al. 128835, NY, US), whereas the rupicolous plants generally have more expanded leaf tissue (0.2–0.5 mm wide on each side of the costa, 0.2–0.4 mm wide on each side of the costule), 15–30 segment pairs, and grow in moist or running water (Maguire & Politi 27764, NY; Maguire et al. 29889, NY).

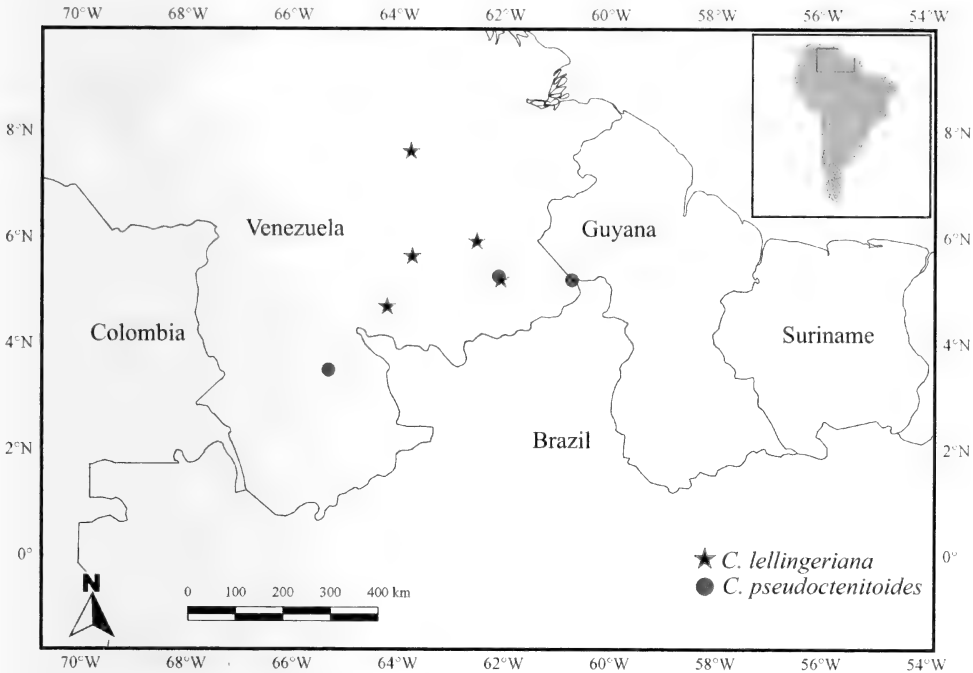


FIG. 22. Distribution of *C. lellingeriana* and *C. pseudoctenitoides*.

*Cyathea asplenioides* shares with *C. universitatis* (Vareschi) Christenh. the presence of one vascular bundle in the petiole in adult plants (White and Turner, 2017).

3. *Cyathea ctenitoides* (Lellinger) Christenh., Phytotaxa 1: 39. 2009. *Hymenophyllopsis ctenitoides* Lellinger, Mem. New York Bot. Gard. 38: 3, fig. 2. 1984. TYPE: VENEZUELA. **Bolívar**: Chimantá Massif, Churi-tepui (Murú-tepui), lower part of lower northwest cumbres, [05°16'N, 61°58'W], 2100–2200 m, 24 Jan 1953, J.J. Wurdack 34175 (holotype: US barcode US0065652!; isotypes: F barcode F0093615, image!, NY barcode NY1731833!, UC barcode UC1503427, image!) (Figs. 12C, D, 13A–E, 14).

**Plants** rupicolous or terrestrial. **Rhizomes** erect, robust, 3.0–8.0 mm diam. (10.0–35.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 10.0–25.0 × 0.1–0.2 mm, concolorous, ferruginous, lustrous, long, linear, twisted at apex, bases truncate, cells of the center of the scale body with thick walls, margins entire, rarely with short setiform projections toward the apex, apices long-filiform (multiseriate). **Leaves** 7.0–26.8 × 1.5–4.4 cm, caespitose, erect, sometimes slightly arching; **petioles** stout, 0.8–1.5 mm diam., 2.4–5.2 cm long, dark brown to dark purple, semi-cylindrical, abaxially rounded, adaxially sulcate, proximal and distal portions densely covered by scales and catenate and clavate hairs, scales of the

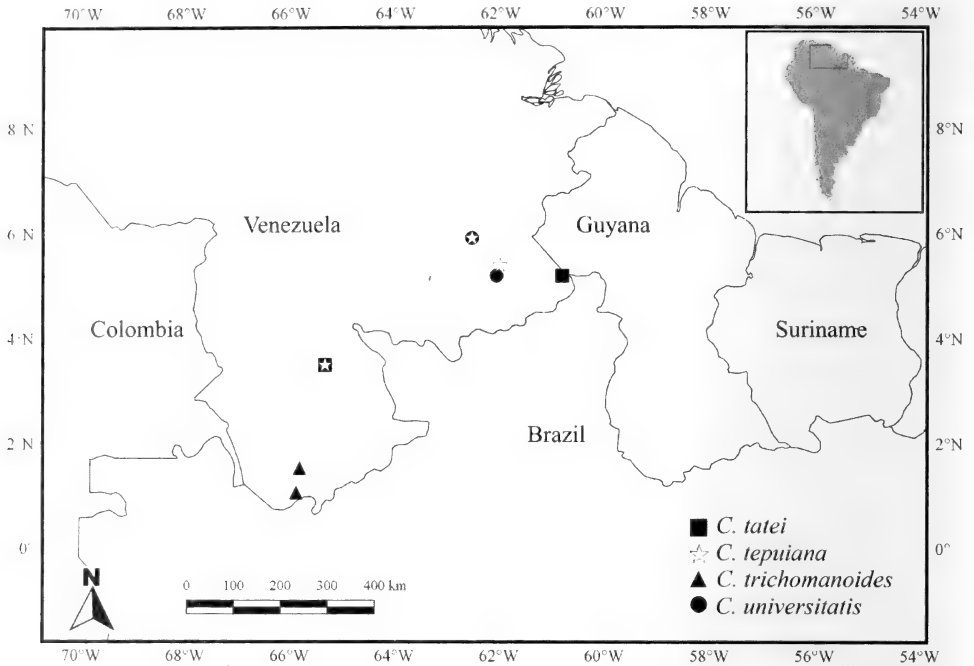


FIG. 23. Distribution of *C. tatei*, *C. tepuiana*, *C. trichomanoides*, and *C. universitatis*.

proximal portion similar to those of the rhizomes, distal ones similar to those of the rachises; **laminae**  $4.4\text{--}17.2 \times 1.5\text{--}4.4$  cm, 3- or 4-pinnate-pinnatisect at base, 2- or 3-pinnate-pinnatisect distally, lanceolate, congested, proximal and distal pinnae reduced, proximal segments overlapping the rachis and secondary rachis; **rachises** abaxially rounded, adaxially 2-sulcate, not winged at base, winged distally, the wings  $0.05\text{--}0.1$  mm wide, densely covered by two kinds of scales and two kinds of hairs, on both surfaces, the scales lanceolate  $2.5\text{--}3.8 \times 0.1\text{--}0.15$  mm, concolorous, ferrugineous, lustrous, twisted, bases truncate, cells of the center of the scale body with thick walls, margins with sparse setiform projections, apices long-filiform (multiseriate), the scales arachnoid,  $1.5\text{--}2.2 \times 0.05\text{--}0.1$  mm, concolorous, ferrugineous, lustrous, twisted, bases truncate, cells of the scale body with thick walls, margins with sparse setiform projections, apices acute (uniseriate), ca.  $0.1$  mm long, ferrugineous, the hairs catenate,  $0.8\text{--}1.4$  mm long, brown, twisted, apices rounded, the hairs clavate,  $0.15\text{--}0.25$  mm long, reddish brown, apices rounded; **pinnae**  $1.0\text{--}2.5 \times 0.5\text{--}1.0$  cm, triangular-lanceolate or lanceolate, congested, 12–30 pairs, alternate, sub-opposite at base, patent; **secondary rachises** with scales and hairs similar to those of rachises on both surfaces; **pinnules** entire, pinnate to pinnatisect, two or three pairs of lateral veins, veins alternate, simple or furcate; **laminar tissue** reduced,  $0.05\text{--}0.2$  mm wide on each side of the secondary rachis,  $0.2\text{--}0.3$  mm wide on each side of the costule; **ultimate segments** with entire margins, apices rounded; **sterile segments**  $0.4\text{--}$

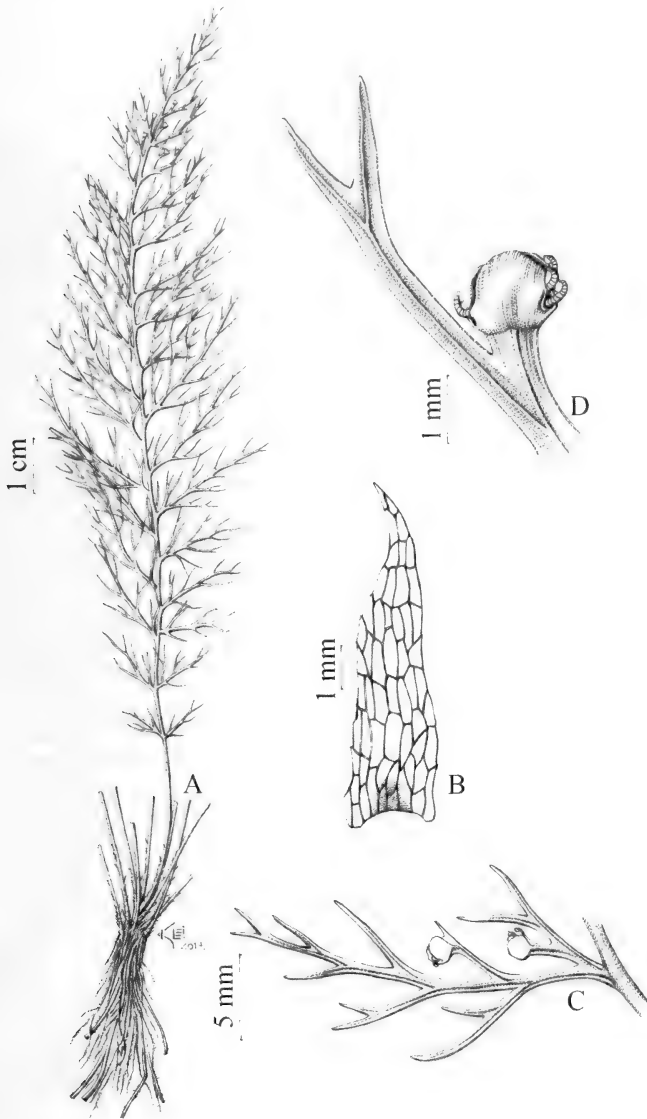


FIG. 24. A–D: *Cyathea tepuiana*. A. Habit. B. Rhizome scale. C. Pinna abaxially. D. Indusium and margin of the lamina (Steysmark 75644, isotype US).

0.6 mm wide; **fertile segments** 0.2–0.5 mm wide. **Sori** 12–52 per pinna, immersed in the laminar tissue, rarely prominent, borne at acroscopic and basiscopic bases of the proximal and distal segments, sometimes along the entire pinna; **indusia** robust, cyatheoid, 1.0–1.4 mm long, margin entire, sinuose, slightly denticulate-lobed; **spores** 64 per sporangium, 42–44  $\mu\text{m}$  in diam., hyaline, surface verrucate and aperture inconspicuous.

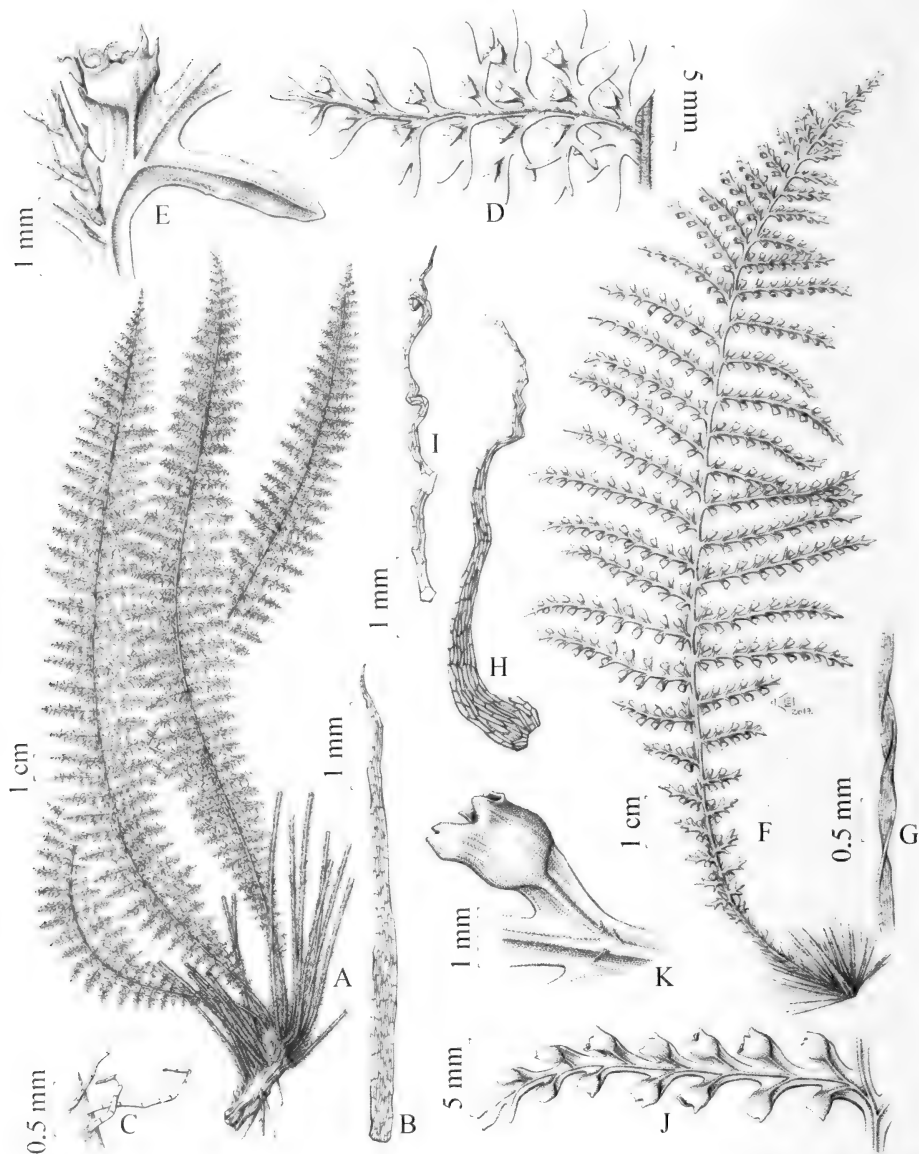


FIG. 25. A–E: *Cyathea trichomanoides*. A. Habit. B. Rhizome scale. C. Hairs from petiole. D. Pinna abaxially. E. Indusium and margin of the lamina. F–K: *C. universitatis*. F. Habit. G. Detail of a rhizome scale. H. Rhizome scale. I. Rachis scale. J. Segment abaxially. K. Indusium (A–E: Maguire et al. 42250, holotype US. F–K: Vareschi & Foldats 4938, isotype US).

*Distribution and ecology.*—*Cyathea ctenitoides* occurs in Brazil (Roraima), Venezuela (Amazonas and Bolívar), and Guyana (Cuyuni-Mazaruni). It grows at the top of the Cerro Marahuaca, Mount Roraima, Ilú-tepui (Ilú-Tramén Massif) and in five mountains of Massif Chimantá (Abácapa-tepui, Apacará-



tepui, Chimantá-tepui, Murú-tepui, and Torono-tepui), on cliff edges, cliffs, flooded places, or close to shrub vegetation in rocky outcrops, in open places, on or below the rocks, forming large populations, mainly in the crevices of shaded rocks; 2100–2850 m elevation.

*Specimens examined*.—VENEZUELA. **Amazonas**: Atabapo, Cerro Marahuaca cumbre, sección noroccidental, 03°30'N, 65°26'W, 2500 m, 16 Feb 1981, *J.A. Steyermark et al. 124361 p.p.* (RB). **Bolívar**: Ilú-tepui, lower plateau, 05°25'N, 60°29'W, 2500 m, 15 Apr 1988, *R. Liesner 23337* (NY); Chimantá Massif, Torono-tepui, summit, at edge escarpment in and among zanjones, [05°24'N, 62°00'W], 2165–2180 m, 9 Feb 1955, *J.A. Steyermark & J.J. Wurdack 636* (NY); Piar, Macizo del Chimantá, altiplanicie meridional del Abácapa-tepui, ubicada en el sector SW del macizo, 05°10'N, 62°16'W, 2200 m, 31 Jan–2 Feb 1984, *O. Huber & N. Dezzio 8660* (NY); idem, sección septentrional del Apacará-tepui, en extremo norte del macizo, 05°25'N, 62°11'W, 2350 m, 3–5 Feb 1984, *O. Huber & M. Colella 8712* (US); idem, altiplanicies en la base meridional de los farallones superiores del Apacará-tepui, sector Norte del macizo, 05°20'N, 60°12'W, 2200 m, 30 Jan–1 Feb 1983, *J.A. Steyermark et al. 128444* (NY); idem, sección oriental del Chimantá-tepui, cabeceras del afluente derecho superior del Río Tirica (“Caño del Grillo”), 05°18'N, 62°03'W, 2450 m, 7–9 Feb 1983, *J.A. Steyermark et al. 128956* (NY).

GUYANA. [**Cuyuni-Mazaruni**]: Summit Roraima, [05°13'N, 60°43'W], 8600 ft. [2621 m], 1808, *M.F.V. McConnell & J.J. Quelch 626* (NY).

BRAZIL. [**Roraima**]: Roraima, [05°12'N, 60°44'W], 2850 m, 1927, *P. Luetzelburg 21638* (NY); idem, Parque Nacional do Monte Roraima, alrededores do acampamento “Guacharo”, 05°09'11"N, 60°43'28"W, 2581 m, 15 Aug 2016, *S. Maciel & P.L. Viana 1852* (SP); idem, caverna próxima à trilha em direção a tríplice fronteira, 05°11'05"N, 60°44'21"W, 2597 m, 16 Aug 2016, *S. Maciel & P.L. Viana 1857, 1861* (SP); idem, entorno do Lago Gladys, 05°14'24"N, 60°44'12"W, 2555 m, 17 Aug 2016, *S. Maciel & P.L. Viana 1867* (SP).

*Cyathea ctenitoides* is characterized by its robust rhizome, 10.0–35.0 mm in diam., including the roots, petioles, and scales (Fig. 13A), which is covered by scales, the scales long, linear, ferruginous, 10.0–25.0 × 0.1–0.2 mm (Fig. 13B). In addition, it has the proximal and distal pinnae reduced, the pinnae congested (Fig. 13A), patent with pendent apex, and rachises densely covered by two kinds of scales (lanceolate and arachnoid, Fig. 13C) and two kinds of hairs (catenate and clavate).

*Cyathea ctenitoides* shares with *C. universitatis* numerous and long scales on the rhizome. However, *C. universitatis* differs in having lamina 3-pinnatisect (vs. 3- or 4-pinnate-pinnatisect in *C. ctenitoides*), sparse (vs. congested), patent pinnae (vs. recurved), and 6–23 sori per segment (vs. 12–52).

4. *Cyathea cylindrica* S. Maciel & Lehnert, Phytotaxa 329(2): 162, figs. 1E–I, 3. 2017. TYPE: VENEZUELA. **Amazonas**: Atabapo. Plateau of Cerro de Marahuaca above Salto Los Monos on tributary of headwaters of Río

Iguapo, 03°37'N, 65°23'W, 2555 m, 26 Feb 1985, *R.L. Liesner 17989* (holotype: US barcode US00785475!; isotypes: MO, not seen, VEN, not seen) (Figs. 11, 12E, 15A–E).

**Plants** rupicolous. **Rhizomes** erect, sometimes suberect, 1.2–2.5 mm diam. (3.7–5.4 mm diam., including the roots; petioles, and scales), scaly, surface of the rhizome usually visible, the scales  $1.5\text{--}2.2 \times 0.2\text{--}0.3$  mm, bicolorous, brown with a dark brown central strip, slightly lustrous, lanceolate, slightly twisted, bases truncate, cells of the center of the scale body with thick walls, margins light brown, with short teeth at base and sparse, short, setiform projections toward the apex, apices attenuate (formed by one cell), brown to dark brown. **Leaves**  $2.3\text{--}10.0 \times 0.6\text{--}2.4$  cm, caespitose, erect; **petioles** slender,  $0.2\text{--}0.5\text{--}(0.7)$  mm diam.,  $0.6\text{--}5.0$  cm long, dark brown to dark purple, cylindrical, proximal portion with sparse scales, similar to those of the rhizomes, narrower, twisted and lustrous, distally with sparse catenate and clavate hairs; **laminae**  $1.7\text{--}5.0 \times 0.6\text{--}2.4$  cm, 3- or 4-pinnate-pinnatisect at base, 3-pinnate-pinnatisect distally, lanceolate, congested, proximal pinnae slightly reduced, distal pinnae gradually reduced, proximal segments overlapping the rachis and secondary rachis; **rachises** rounded on both surfaces, sometimes slightly sulcate adaxially, not winged, sometimes distally winged, the wings inconspicuous, ca. 0.05 mm wide, with two kinds of hairs, catenate and clavate, sparse on both surfaces, the catenate hairs ca. 1 mm long, brown, apices acute, the clavate hairs 0.1–0.2 mm long, reddish brown, apex rounded; **pinnae** cylindrical, ca.  $1.2 \times 0.8$  cm, lanceolate, congested, 7–12 pairs, alternate, almost sub-opposite at base, usually patent, sometimes ascending distally; **secondary rachises** usually glabrous on both surfaces, seldom with sparse clavate hairs on both surfaces; **pinnules** cylindrical, entire, pinnate, occasionally slightly pinnatisect, with one pair of lateral veins, veins alternate, simple or furcate; **laminar tissue** inconspicuous, ca. 0.05 mm wide on each side of the secondary rachis and ca. 0.05 mm wide on each side of the costule; **ultimate segments** usually cylindrical, margins entire, apex rounded; **sterile segments** 0.2–0.4 mm wide; **fertile segments** 0.3–0.4 mm wide. **Sori** 1–6 per pinna, usually immersed in the laminar tissue, rarely prominent, borne at acroscopic and basiscopic bases of the proximal and distal segments; **indusia** mostly bivalvate, adaxial valve ca. 0.9 mm long, margin subentire to triangular-lobed, abaxial valve ca. 0.5 mm long, margin subentire to repand, rarely appearing cyatheoid if valves very short, then cup ca. 0.5 mm long, margins subentire to triangular-lobed; **spores** 32 per sporangium, ca. 52  $\mu\text{m}$  in diam., yellowish, surface rugate and aperture conspicuous.

*Distribution and ecology.*—*Cyathea cylindrica* occurs at high elevations (1850–2555 m) in Venezuela (Amazonas and Bolívar) and Brazil (Amazonas), in the tepuis Amurí-tepui and Churí-tepui (Massif of Chimantá), Pico da Neblina, and Marahuaca. It grows as erect tufts, in sandstone outcrops, close to flooded areas, in the damp walls of shaded cliffs, and along streams, especially in the cracks of rocks.

*Specimens examined*.—VENEZUELA. [**Amazonas**]: Cerro de la Neblina, Venezuelan-Brazilian frontier, planicie de Zuloaga, Río Titirico, [01°04'N, 66°09'W], 2300 m, 10–15 Oct 1970, *J.A. Steyermark 103891 p.p.* (NY); idem, id., 2300 m, 10–15 Oct 1983, *J.A. Steyermark 103893* (NY). **Bolívar**: Piar. Macizo del Chimantá, pequeñas altiplanicies em la base septentrional de los farallones superiores del Amurí-tepui (sector W del Acopán-tepui), 05°10'N, 62°07'W, 1850 m, 2–5 Feb 1983, *J.A. Steyermark et al. 128605* (NY); idem, id., sector SE, altiplanicie levemente inclinada hacia el SSE ubicada en la sección centro-suroriental del Churí-tepui, 05°15'N, 61°58'W, 1850 m, 10–12 Feb 1984, *O. Huber & M. Colella 8988* (NY).

BRAZIL. **Amazonas**: Santa Isabel do Rio Negro. Parque Nacional do Pico da Neblina, trilha para a cachoeira do Anta, alto da Serra da Neblina, acampamento do Marco 5 da fronteira Brasil com a Venezuela, 00°00'N, 65°00'W, 2343 m, 31 Dec 2004, *F.A. Carvalho et al. 372* (INPA).

*Cyathea cylindrica* is easily recognized by cylindrical pinnae and pinnules (Fig. 15A, C). It is also distinguishable by the rachises with both catenate and clavate hairs, sparse on both surfaces (Fig. 15D), and by the bicolorous rhizome scales, with short teeth at the base and sparse, short, setiform projections toward the apex (Fig. 15B).

The specimen *Liesner 17989* (MO, US, VEN) was interpreted as an atypical form of *Hymenophyllopsis steyermarkii* ( $\equiv$  *C. tepuiana*) by White and Turner (2017). However, this material was selected as the type of *C. cylindrica*, a new species recently described by Maciel *et al.* (2017), which differs in having pinnae and pinnules cylindrical, exactly the distinct character cited by White and Turner (2017: p. 35, 40, Fig. 1C).

According to Maciel *et al.* (2017), specimens of *C. cylindrica* were also treated as *C. dejecta* and *C. hymenophylloides* by White and Turner (2017). However, *C. dejecta* differs by the concolour rhizome scales (vs. bicolorous in *C. cylindrica*) and rachises with scales and hairs (vs. only hairs). *Cyathea hymenophylloides* has glabrous rachises or only with clavate hairs (vs. catenate and clavate hairs in *C. cylindrica*), concolourous rhizome scales and margins generally entire (vs. bicolorous rhizome scales and margins present short teeth at base and sparse, short, setiform projections toward the apex).

5. *Cyathea dejecta* (Baker) Christenh., Phytotaxa 1: 39. 2009. *Hymenophyllum dejectum* Baker. Icon. Pl. 17, fig. 1610. 1886. *Hymenophyllopsis dejecta* (Baker) K. I. Goebel., Flora 124: 3: 1929. *Asplenium dejectum* (Baker) Pittier, Cat. Fl. Venez. 46: 1945. TYPE: VENEZUELA. [**Bolívar**]: Mount Roraima, [05°12'N, 60°44'W], Dec 1884, *E.F. in Thurn 318* (holotype: K barcode K000589730, image!; isotype: US barcode US00065653!) (Figs. 12G, H, 14, 16A–F).

**Plants** rupicolous. **Rhizomes** erect, 2.4–4.0 mm diam. (6.0–25.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 1.3–6.0  $\times$  0.2–0.5 mm, concolourous, light brown or brown, opaque, lanceolate, twisted, base truncate, cells of the scale body with thick

walls, margins entire or with sparse, short, setiform projections, apices acuminate or attenuate (formed by one cell). **Leaves** 5.0–21.0 × 1.5–3.0 cm, caespitose, erect; **petioles** stout, 0.7–1.8 mm diam., 1.0–9.0 cm long, dark brown to dark purple, semi-cylindrical, abaxially rounded, adaxially sulcate, proximal and distal portions densely covered by scales, the proximal scales similar to those of the rhizomes, the distal scales narrow and twisted; **laminae** 4.0–15.0 × 1.5–3.0 cm, 3–5-pinnate-pinnatisect at base, 2–4-pinnate-pinnatisect distally, usually narrow-lanceolate, occasionally lanceolate, congested, proximal pinnae usually unreduced, distal pinnae gradually reduced, proximal segments overlapping the rachis and secondary rachis; **rachises** usually abaxially rounded and adaxially 2-sulcate, not winged or distally winged, the wings 0.05–0.1 mm wide, with one kind of scale and two kinds of hairs on both surfaces, the scales 0.8–2.5 × 0.2–0.3 mm, concolorous, lanceolate, light brown to brown, opaque, twisted, bases truncate or rounded with the center dark brown, cells of the scale body with thick walls, margins with sparse, short, setiform projections at base and toward the apex, apices attenuate (formed by one cell), brown to reddish brown, the catenate hairs, 0.4–1.2 mm long, brown to reddish brown, twisted, apex rounded or acute, the clavate hairs, 0.1–0.2 mm long, reddish brown, apices rounded; **pinnae** 0.8–2.8 × 0.4–1.5 cm, lanceolate, usually congested, sometimes slightly sparse, 12–40 pairs, usually alternate, opposite at base, patent, with apices recurved; **secondary rachises** usually with scales and catenate hairs similar to those of rachises on both surfaces, sometimes glabrous on the adaxial surface; **pinnules** entire, pinnate to pinnatisect, two or three pairs of lateral veins, veins alternate, simple or furcate; **laminar tissue** slightly reduced, 0.05–0.2 mm wide on each side of the secondary rachis, 0.1–0.4 mm wide on each side of the costule; **ultimate segments** with entire margins, sinuose, apex usually acute or rounded; **sterile segments** 0.2–0.8 mm wide; **fertile segments** 0.2–0.4 mm wide. **Sori** 2–18 per pinna, usually prominent in the laminar tissue, rarely immersed, borne at acroscopic and basiscopic bases of the proximal and distal segments; **indusia** robust, cyatheoid, 0.6–1.0 mm long, margin deeply denticulate-lobed, sometimes sinuose or slightly lacerate; **spores** 64 per sporangium, 44–55 µm in diam., hyaline, surface rugate (with rodlets) and aperture conspicuous.

*Distribution and ecology.*—*Cyathea dejecta* occurs in Northern Brazil (Roraima), Guyana (Cuyuni-Mazaruni), and Venezuela (Bolívar) where it grows at high elevations (2551–2800 m) in the following tepuis: Roraima Mount, Kukenán, Ilú-tepui (Massif Ilú-Tramén), and Marahuaca. It prefers growing in rocky plateaus of open areas, beneath of herbaceous-shrub vegetation on dry rocks, on the edges of caves, on and under rocks, and in cracks and fissures.

*Specimens examined.*—VENEZUELA. **Bolívar:** Roscio, cumbre del Ilú-(Uru-)tepui, sector centromeridional, 05°25'N, 60°59'W, 2630 m, 29 Apr 1984, *O. Huber 9515* (NY); idem, Kukenán-(Matauí)-tepui, cumbre meridional cerca de la punta Sur del Tepui, 05°12'N, 60°49'W, 15 June 1985, *O. Huber & C. Alarcon 10542* (NY); Cerro Roraima, cumbre, parte noreste de Venezuela

imediate al sur del hito que marca los limites con Guyana, Brasil y Venezuela, 05°12'N, 60°42'W, 2750–2800 m, 26 Aug–2 Sep 1976, *J.A. Steyermark et al.* 112516, 112569 (NY, US).

GUYANA. [**Cuyuni-Mazaruni**]: Roraima, [05°12'N, 60°44'W], 1895, *G.S. Jenman s.n.* (NY).

BRAZIL. **Roraima**: Parque Nacional do Monte Roraima, arredores do acampamento “Guacharo”, 05°09'11"N, 60°43'28"W, 2581 m, 15 Aug 2016, *S. Maciel & P.L. Viana 1853* (SP); idem, caverna próxima à trilha em direção a tríplice fronteira, 05°11'05"N, 60°44'21"W, 2597 m, 16 Aug 2016, *S. Maciel & P.L. Viana 1860* (SP); idem, arredores da tríplice fronteira, 05°12'06"N, 60°44'15"W, 2583 m, 18 Aug 2016, *S. Maciel & P.L. Viana 1868, 1869* (SP); idem, trilha próxima ao acampamento Quati, 05°12'38"N, 60°43'52"W, 2551 m, 19 Aug 2016, *S. Maciel & P.L. Viana 1876* (SP).

*Cyathea dejecta* is characterized by a narrow-lanceolate lamina, pinnae patent with apices recurved (Fig. 16A), proximal pinnae unreduced (Fig. 16A), petioles adaxially sulcate (Fig. 16C), and secondary rachises with opaque scales and catenate hairs on both surfaces, sometimes glabrous on the adaxial side.

*Cyathea dejecta* is generally confused with *C. ctenitoides*, *C. cylindrica* (see comments under that species), and *C. hymenophylloides*, which has resulted in erroneous interpretations of its circumscription (Goebel, 1929; Smith, 1930; Lellinger, 1984, 1991, 1995; White and Turner, 2017). *Cyathea ctenitoides* is distinct in its rachises with two kinds of scales, lanceolate and arachnoid (vs. lanceolate scales only, in *C. dejecta*) and rhizome scales lustrous, ferrugineous, 10.0–25.0 mm long (vs. opaque, light brown or brown, 1.3–6.0 mm long). *Cyathea hymenophylloides* differs by the sparse laminae and pinnae with patent apices (vs. laminae congested and pinnae with recurved apices in *C. dejecta*), rachises adaxially rounded, glabrous or with sparse clavate hairs on both surfaces (vs. rachises adaxially sulcate, with scales and two kinds of hairs, catenate and clavate, on both surfaces), slender petioles, 0.2–0.5 mm in diam. (vs. stout, 0.7–1.8 mm diam.), bivalvate indusia (vs. cyatheoid), and short-creeping rhizomes (vs. erect).

Recently, Maciel *et al.* (2017) published a new species (*C. cylindrica*) segregated from *C. dejecta* and, in this work, we are also proposing three other new species, also segregated from *C. dejecta* (*C. indefinita*, *C. minima*, and *C. tatei*), based on morphological and molecular data (unpublished), with the aim of providing a better circumscription for *C. dejecta*.

6. *Cyathea hymenophylloides* (L. D. Gómez) Christenh., Phytotaxa 1: 39. 2009. *Hymenophyllopsis hymenophylloides* L. D. Gómez, Revista Biol. Trop. 21: 103, figs. 1, 2. 1973. TYPE: VENEZUELA. **Bolívar**: Cerro Venamo, parte Sur-Oeste, cerca de los limites con la Guayana Inglesa, [05°57'N, 61°23'W], 1500 m, 02 Jan 1964, *J.A. Steyermark, G.C.K & E. Dunsterville 92584* (holotype: F barcode F0075727, image!; isotypes: CR barcode CR242825, image!, GH barcode GH00021314, image!, NY barcode NY02713267!, VEN barcode VEN282742, image!) (Figs. 14, 17A–D, 18A, B).

**Plants** rupicolous or terrestrial. **Rhizomes** short-creeping, 1.0–1.7 mm diam. (2.0–5.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome slightly visible, the scales  $0.7\text{--}1.2 \times 0.15\text{--}0.25$  mm, concolorous, dark brown, lustrous, oval-lanceolate, twisted, bases rounded, cells of the scale body with thick walls, margins entire or rarely with some short setiform projections toward the apex, apices short-attenuate (formed by one cell), reddish brown. **Leaves**  $6.0\text{--}20.5 \times 1.8\text{--}4.0$  cm, caespitose, erect; **petioles** slender, 0.2–0.5 mm diam., 2.5–9.3 cm long, dark brown to dark purple, cylindrical, scales of the proximal portion similar to those of the rhizome, narrower and twisted, distally glabrous or with sparse clavate hairs; **laminae**  $6.0\text{--}16.5 \times 1.8\text{--}4.0$  cm, 3- or 4-pinnate-pinnatisect at base, 3-pinnate-pinnatisect distally, lanceolate, sparse, proximal pinnae slightly reduced, distal pinnae gradually reduced, proximal segments overlapping the rachis; **rachises** rounded on both surfaces, not winged, sometimes inconspicuously winged distally, the wings ca. 0.05 mm wide, glabrous on both surfaces or with sparse clavate hairs on both surfaces, 0.1–0.2 mm long, brown, apices rounded; **pinnae**  $1.2\text{--}2.0 \times 0.5\text{--}0.8$  cm, triangular-lanceolate, sparse, 15–32 pairs, usually alternate, almost sub-opposite at base, pinnae patent, sometimes distal pinnae slightly ascending; **secondary rachises** usually glabrous on both surfaces, sometimes with sparse clavate hairs on both surfaces; **pinnules** entire, pinnatisect to pinnate, with one or two pairs of lateral veins, veins alternate, furcate; **laminar tissue** reduced, 0.05–0.1 mm wide on each side of the secondary rachis, 0.1–0.2 mm wide on each side of the costule; **ultimate segments** with entire margins, apices rounded; **sterile segments** 0.3–0.4 mm wide; **fertile segments** 0.3–0.4 mm wide. **Sori** 9–33 per pinna, immersed in the laminar tissue, rarely prominent, borne at acroscopic and basiscopic bases of the proximal and distal segments; **indusia** fragile, bivalvate, adaxial and abaxial valves 0.4–0.6 mm long, margins deeply lacerate, sometimes widely denticulate-lobed; **spores** 64 per sporangium, 43–44  $\mu\text{m}$  in diam., hyaline, surface verrucate (with rodlets) and aperture inconspicuous.

*Distribution and ecology.*—*Cyathea hymenophylloides* occurs in northern Brazil (Amazonas), Venezuela (Amazonas and Bolívar), and probably in Guyana. It grows near streams, over mosses, forming tufts on the dry face of the rock or on small shady cliffs; 1220–1850 m elev.

*Specimens examined.*—VENEZUELA. **Amazonas:** Río Negro, Cerro Aracamuni, summit, proa camp,  $01^{\circ}32'\text{N}$ ,  $65^{\circ}49'\text{W}$ , 1400 m, 28 Oct 1987, R. Liesner & G. Carvenali 22568 (NY). **Bolívar:** Cerro Guaiquinima, cumbre, sector suroeste, cerca del borde,  $05^{\circ}38'\text{N}$ ,  $63^{\circ}45'\text{W}$ , 1650 m, 26 May 1978, J.A. Steyermark et al. 117447 (US); Cerro Venamo (parte Sur-Oeste), cerca de los límites con la Guayana Inglesa, [ $05^{\circ}57'\text{N}$ ,  $61^{\circ}23'\text{W}$ ], 1220–1275m, 6–7 Jan 1964, J.A. Steyermark et al. 92730 (NY, US). Piar, Macizo del Chimantá, pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (sector W del Acopán-tepui),  $05^{\circ}10'\text{N}$ ,  $62^{\circ}07'\text{W}$ , 1850 m, 2–5 Feb 1983, J.A. Steyermark et al. 128482 (NY, US).

**BRAZIL. Amazonas:** Plateau of northern massif of Serra do Aracá, north part of northern mountain near peak,  $00^{\circ}51'\text{--}57'\text{N}$ ,  $63^{\circ}21'\text{--}22'\text{W}$ , 1400 m, 18 Feb

1984, *G.T. Prance et al.* 29149 (INPA, MG, NY). Barcelos, Parque Estadual da Serra do Aracá, floresta nebular próxima de curso d'água, 00°55'54"N, 63°21'34"W, 1400 m, 30 Sep 2011, *R.C. Forzza et al.* 6597 (RB, SP).

*Cyathea hymenophylloides* is characterized by the short-creeping rhizomes (Fig. 17A), laminae 3- or 4-pinnate-pinnatisect, and with reduced laminar tissue (0.05–0.1 mm wide on each side of the secondary rachis). The rhizome scales are oval-lanceolate, concolorous (Fig. 17B), and bivalvate indusia, with deeply lacerate valves (Fig. 17D).

*Cyathea hymenophylloides* is similar to *C. lellingeriana*, a recently described species (Maciel *et al.*, 2017), because both have bivalvate indusia generally with the margins of the valve deeply lacerate. However, *C. lellingeriana* can be distinguished by the erect to suberect rhizomes and bicolorous rhizome scales (vs. short-creeping and concolorous).

7. *Cyathea incognita* (Lellinger) Christenh., *Phytotaxa* 1: 41. 2009. *Hymenophyllopsis incognita* Lellinger, *Mem. New York Bot. Gard.* 38: 6, fig. 3. 1984. TYPE: VENEZUELA. **Bolívar**: Meseta del Jáua, Cerro Jáua, cumbre de la porción central-occidental de la meseta, 36 millas náuticas o 60 kms, noroeste de la misión de campamento sanidad del Río Kanarakuni, 04°45'N, 64°26'W, 1922–2100 m, 22–27 Mar 1967, *J.A. Steyermark 98014* (holotype: US barcode US00065654!; isotype: NY barcode NY00144735!) (Figs. 12F, 14, 17E–H).

**Plants** rupicolous. **Rhizomes** erect, 1.4–1.8 mm diam. (2.3–7.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 1.5–3.0 × 0.1–0.2 mm, concolorous, light brown to brown, lustrous, lanceolate, twisted, bases truncate, cells of the scale body with thick walls, margins entire, apices acute (formed by one cell), 0.15–0.2 mm long, reddish brown. **Leaves** 3.6–13.4 × 0.7–3.8 cm, caespitose, erect to pendent; **petioles** slender, 0.2–0.5 mm diam., 1.5–6.0 cm long, dark brown to dark purple, cylindrical, scales of the proximal portion similar to those of the rhizome, narrower and twisted, distally with sparse clavate hairs; **laminae** 2.0–9.7 × 0.7–3.8 cm, 3- or 4-pinnate-pinnatisect at base, 2-pinnate-pinnatisect distally, lanceolate, sparse, proximal pinnae unreduced or slightly reduced, distal pinnae gradually reduced, proximal segments overlapping the rachis; **rachises** rounded on both surfaces, not winged at base, distally winged, the wings 0.05–0.2 mm wide, glabrous on both surfaces or with sparse clavate hairs on both surfaces, 0.1–0.2 mm long, brown, apices rounded; **pinnae** 0.5–1.6 × 0.4–1.0 cm, triangular-lanceolate, sparse, 7–22 pairs, alternate, almost sub-opposite at base, pinnae usually ascending, sometimes patent; **secondary rachises** usually glabrous on both surfaces, sometimes with few clavate hairs on both surfaces; **pinnules** entire, pinnatisect, one pair of lateral veins, veins alternate, simple or furcate; **laminar tissue** broad, 0.1–0.35 mm wide on each side of the secondary rachis, 0.3–0.5 mm wide on each side of the costule; **ultimate segments** with entire margins, sometimes subentire, apices rounded to acute; **sterile segments** 0.7–1.0 mm wide; **fertile segments** 0.3–0.4 mm wide.

**Sori** 1–11 per pinna, usually immersed in the laminar tissue, rarely prominent, borne at the acroscopic and basiscopic bases of the proximal and distal segments; **indusia** robust, bivalvate, adaxial and abaxial valves 0.6–1.0 mm long, margins broadly denticulate-lobed, sometimes deeply lacerate; **spores** 32 per sporangium, ca. 60  $\mu\text{m}$  in diam., orangish, surface rugate and aperture inconspicuous.

*Distribution and ecology.*—*Cyathea incognita* occurs only in Venezuela (Bolívar), in the tepuis Agparamán (Massif Chimantá) and Cerro Jáua. It grows in ravines along rocky streams, in crevices of shady rocks; 1880–2100 m elev.

*Specimens examined.*—VENEZUELA. **Bolívar:** Chimantá Massif, Agparamán-tepui, southeast facing forested slopes below escarpment, [05°14'N, 62°12'W], 1880–1955 m, 26 Feb 1955, J.A. Steyermark & J.J. Wurdack 1141 (NY).

*Cyathea incognita* is recognized by the laminae 3- or 4-pinnate-pinnatisect, proximal pinnae unreduced or slightly reduced (Fig. 17E). The laminar tissue is broad, 0.1–0.35 mm wide, on each side of the secondary rachis, 0.3–0.5 mm wide on each side of the costule (Fig. 17 G), the petioles are slender (0.2–0.5 mm diam.), and the rhizome scales have entire margins (Fig. 17F).

*Cyathea incognita* is similar to *C. hymenophylloides* in lamina dissection. However, *C. hymenophylloides* differs by the short-creeping rhizome and the oval-lanceolate scales (vs. erect and lanceolate).

8. *Cyathea indefinita* S. Maciel & J. Prado, **sp. nov.** TYPE: VENEZUELA. **Bolívar:** Cerro Roraima, cumbre, parte noreste da Venezuela inmedata al sur del hito que marca los limites com Guyana, Brasil y Venezuela, 05°12'N, 60°42'W, 2750–2800 m, 26 Aug–2 Sep 1976, J.A. Steyermark, C. Brewer-Carías, G.C.H. & E. Dunsterville 112515 (holotype: NY barcode NY02713284!; isotypes: NY barcode NY02713283!, VEN, not seen) (Figs. 19A–G, 20, 21A, B).

*Diagnosis.*—*Cyathea indefinita* can be recognized by the congested 4-pinnate-pinnatisect laminae, rachises with bullate scales and hairs of two kinds (catenate and clavate) on both surfaces, secondary rachises glabrous adaxially and with catenate and clavate hairs abaxially. The sori are usually prominent in the laminar tissue and the indusia are cyatheoid.

**Plants** rupicolous. **Rhizomes** erect, 3.0–4.4 mm diam. (9.2–17.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 1.6–3.0  $\times$  0.2–0.25 mm, concolorous, paleaceous, opaque, lanceolate, not twisted, bases truncate, sometimes bases rounded, cells of the scale body with thick walls, margins entire, with few short setiform projections toward the apex, apices acute (uniseriate), ca. 0.15 mm long, hyaline. **Leaves** 9.0–25.0  $\times$  2.0–5.0 cm, caespitose, erect; **petioles** stout, 0.6–1.8 mm diam., 3.0–11.0 cm long, dark brown to dark purple, semi-cylindrical, abaxially rounded, adaxially sulcate, proximal and distal portions covered by scales similar to those of the rhizomes, twisted; **laminae** 9.0–15.7  $\times$  2.0–5.0 cm, 4-pinnate-pinnatisect at base, 3- or 4-pinnate-pinnatisect distally, lanceolate, congested,



proximal and distal pinnae reduced, proximal segments overlapping the rachis and secondary rachis; **rachises** abaxially rounded, adaxially 2-sulcate, not winged, sometimes inconspicuously winged distally, the wings ca. 0.05 mm wide, with one kind of scale and two kinds of hairs on both surfaces, the scales  $1.5\text{--}3.8 \times 0.2\text{--}0.25$  mm, concolorous, brown, lustrous, bullate, twisted, bases rounded with the center dark brown, cells of the scale body with thick walls, margins sparsely denticulate, apices long-filiform (multiseriate), the catenate hairs 0.4–2.0 mm long, brown, twisted, apices acute, the clavate hairs 0.1–0.15 mm long, reddish brown, apices rounded; **pinnae**  $1.0\text{--}2.5 \times 0.6\text{--}1.5$  cm, lanceolate, congested, 18–25 pairs, usually alternate, almost sub-opposite at base, patent; **secondary rachises** adaxially glabrous, abaxially with catenate and clavate hairs, similar to those of the rachises; **pinnules** entire, pinnatisect to pinnate, with one or three pairs of lateral veins, veins alternate, simple or furcate; **laminar tissue** reduced, ca. 0.05 mm wide on each side of the secondary rachis, 0.1–0.2 mm wide on each side of the costule; **ultimate segments** with entire margins, apices rounded; **sterile segments** 0.3–0.5 mm wide; **fertile segments** 0.2–0.3 mm wide. **Sori** 8–15 per pinna, usually prominent in the laminar tissue, rarely immersed, borne at the acroscopic and basiscopic bases of the proximal and distal segments; **indusia** fragile, cyatheoid, 0.2–1.0 mm long, margin usually subentire to sinuose, sometimes denticulate-lobed; **spores** 64 per sporangium, 46–53  $\mu\text{m}$  in diam., yellowish, verrucate, surface finely rugate and aperture conspicuous.

**Distribution and ecology.**—*Cyathea indefinita* occurs only in the tepui Roraima Mount (Brazil, Venezuela, and possibly Guyana). It grows at the edges of caves, in shady places, or in moist rock outcrops, usually in cracks of rocks at high elevations (2597–2740 m elev.).

**Etymology.**—The epithet “*indefinita*” (from Latin *indefinitus* = indeterminate or uncertain) is related to the absence of a characteristic to recognize promptly this taxon.

**Additional specimens examined.**—VENEZUELA. **Bolívar:** Summit of Mount Roraima, on southern half of the summit between summit camp, great central rift, central swamp, and pond at southern end, [05°12'N, 60°44'W], 2700–2740 m, 28 Sep 1944, J.A. Steyermark 58875 p.p. (NY, US).

**BRAZIL. Roraima:** Parque Nacional do Monte Roraima, caverna próxima à trilha em direção a tríptica fronteira, 05°11'05" N, 60°44'21" W, 2597 m, 16 Aug 2016, S. Maciel & P.L. Viana 1855, 1856 (SP).

*Cyathea indefinita* resembles *C. minima* by the laminae 3-pinnate-pinnatisect and the indusia cyatheoid. *Cyathea minima* differs, however, by having smaller leaves,  $3.0\text{--}7.5 \times 0.7\text{--}2.7$  cm (vs. leaves robust,  $9.0\text{--}25.0 \times 2.0\text{--}5.0$  cm in *C. indefinita*; Fig. 19A), shorter petioles, 0.3–3.0 cm long, cylindrical (vs. long petioles, 3.0–11.0 cm long, semi-cylindrical; Fig. 19A, D), pinnae with apex recurved (vs. patent), and rachises with two kind of scales, bullate and lanceolate (vs. only bullate, Fig. 19E).

9. *Cyathea lellingeriana* S. Maciel & J. Prado, Phytotaxa 329(2): 163, figs. 2A–D, 3. 2017. TYPE: VENEZUELA. **Bolívar:** Meseta del Jaua, Cerro Sarisa-

riñama, Cumbre, porción Noreste, quebrada baja em selva más alta de promedio de 15–20 metros de alto, 04°41'40"N, 64°13'20"W, 1400 m, 16–18 Feb 1974, J.A. Steyermark, V.C. Espinoza & C. Brewer-Carías 109201 (holotype: US barcode US00785450!; isotypes: NY barcode NY00144736!, VEN, not seen) (Figs. 15F–J, 18C, D, 22).

**Plants** rupicolous. **Rhizomes** usually erect, sometimes suberect, 1.2–2.4 mm diam. (5.0–12.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome slightly visible, the scales  $1.2\text{--}2.7 \times 0.2\text{--}0.35$  mm, bicolorous, brown, with a central dark brown strip, lustrous, lanceolate to linear-lanceolate, twisted, bases rounded, cells of the center of the scale body with thick walls, margins light brown, entire, apices short-attenuate (formed by one cell), reddish brown. **Leaves**  $3.3\text{--}18.0 \times 0.9\text{--}3.8$  cm, caespitose, erect; **petioles** slender, 0.2–0.3 mm diam., 0.7–8.0 cm long, dark brown to dark purple, cylindrical, scales of the proximal portion similar to those of the rhizomes, narrower and twisted, distally with sparse clavate hairs; **laminae**  $2.6\text{--}10.0 \times 0.9\text{--}3.8$  cm, 5-pinnate-pinnatisect at base, 3- or 4-pinnate-pinnatisect distally, lanceolate, congested, proximal pinnae unreduced, distal pinnae gradually reduced, proximal segments overlapping the rachis and secondary rachis; **rachises** rounded on both surfaces, sometimes abaxially rounded, adaxially slightly complanate, not winged at base, inconspicuously winged distally, the wings ca. 0.05 mm wide, adaxially glabrous, abaxially with sparse, clavate hairs, 0.1–0.2 mm long, brown, apices rounded; **pinnae**  $1.5\text{--}2.5 \times 0.6\text{--}1.0$  cm, triangular-lanceolate, 8–30 pairs per frond, usually alternate, almost sub-opposite at base, pinnae patent; **secondary rachises** adaxially glabrous, abaxially with sparse, clavate hairs; **pinnules** entire, pinnate to pinnatisect, one or two pairs of lateral veins, veins alternate, furcate up to three times, rarely simple; **laminar tissue** slightly broad, 0.1–0.3 mm wide on each side of secondary rachis, 0.2–0.35 mm wide on each side of the costule; **ultimate segments** with crenate to erose margins, apices rounded; **sterile segments** 0.4–0.7 mm wide; **fertile segments** 0.2–0.4 mm wide. **Sori** (6–)18–42 per pinna, usually immersed in the laminar tissue, rarely prominent, borne on the acroscopic and basiscopic bases of the proximal and distal segments; **indusia** fragile, bivalvate, adaxial and abaxial valves ca. 0.5 mm long, margins usually deeply lacerate, sometimes fimbriate; **spores** 64 per sporangium, 40–43  $\mu\text{m}$  in diam., yellowish, surface verrucate and aperture inconspicuous.

*Distribution and ecology.*—*Cyathea lellingeriana* occurs only in Venezuela (Bolívar), in the tepuis Auyán-tepui, Acopán-tepui (Massif of Chimantá), Cerro la Danta, Cerro Guaiquinima, and Cerro Sarisariñama. *Cyathea lellingeriana* grows on rocks or in crevices at the base of the rocks inside the forests, or, commonly, beneath wet rocks covered by mosses; (770–) 1040–1700 elev.

*Specimens examined.*—VENEZUELA. **Bolívar:** Auyán-tepui, cumbre de la parte norte dela sección sur (división occidental del cerro), a lo largo del Río Churún al pie de “Second Wall” de arenisca, desde el campamento norte, 5 kms hacia noroeste, [05°55'N, 62°32'W], 1660 m, 12 May 1964, J.A. Steyermark

93817 (US); Raul Leoni, bosque de altiplanicie en orilla de quebrada, parte N del Macizo Guanacoco, 04°57'N, 63°53'W, 770 m, Nov 1988, *A. Fernandez & G. Aymard* 4850, 4873 (NY); Cerro la Danta, northwest of Cerro Venamo, wooded quebrada, northern slopes, headwaters of Río Venamo, west of vicinity of road campamento 125, [7°36'N, 63°46'], 1040–1060 m, 13 Apr 1960, *J.A. Steyermark & S. Nilsson* 25, 33 (NY); Cerro Guaiquinima, Río Paragua, [05°38'N, 63°45'W], 1600–1700 m, 31 Dec 1951, *B. Maguire* 32895 (NY); Macizo del Chimantá, Acopán-tepui, [05°11'N, 62°00'W], Jun 1997, *P. Wolf* s.n. (UC).

According to Maciel *et al.* (2017), *Cyathea lellingeriana* is distinguished from the other species by the congested laminae (Fig. 15F), segments with crenate to erose margins (Fig. 15I, J), rhizome scales bicolorous, with margins entire (Fig. 15G), and rachises adaxially glabrous and abaxially with sparse clavate hairs (Fig. 15H).

10. ***Cyathea minima*** S. Maciel & J. Prado, **sp. nov.** TYPE: VENEZUELA. **Amazonas:** Río Negro. Neblina Massif, camp 12, Venezuelan-Brazilian frontier, [05°09'N, 60°47'W], 1950 m, 26–27 Feb 1985, *B.M. Boom, W.R. Buck & C. Brewer-Carías* 6014 (holotype: NY barcode NY02566191!; isotype: VEN, not seen) (Figs. 19H–M, 20, 21C, D).

**Diagnosis.**—*Cyathea minima* is characterized by its diminutive leaves, 3.0–7.5 × 0.7–2.7 cm; short (0.3–3.0 cm long) cylindrical petioles; congested laminae; reduced proximal pinnae pair; 11–20 pairs of pinnae, with apices recurved; rachises covered with two kind of scales (lanceolate and bullate) and two kinds of hairs (catenate and clavate), and indusia cyatheoid, with margin denticulate-lobed.

**Plants** rupicolous. **Rhizomes** erect, 3.2–4.0 mm diam. (5.2–7.6 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 2.0–6.0 × 0.15–0.3 mm, concolorous, light brown, lustrous, narrow-lanceolate, slightly twisted, bases truncate, cells of the center of the scale body with thick walls, margins entire, short setiform projections toward the apex, apices acute (uniseriate), ca. 0.15 mm long, brown to reddish brown. **Leaves** 3.0–7.5 × 0.7–2.7 cm, caespitose, erect; **petioles** stout, 0.8–1.7 mm diam., 0.3–3.0 cm long, dark brown to dark purple, cylindrical, sometimes adaxial face complanate distally, proximal and distal portions densely scaly, the scales similar to those of the rhizomes, twisted, with denticulate margins; **laminae** 2.5–7.0 × 0.7–2.7 cm, 4-pinnate-pinnatisect at base, 3-pinnate-pinnatisect distally, lanceolate, congested, proximal and distal pinnae reduced, proximal segments overlapping the rachis and secondary rachis; **rachises** abaxially rounded, adaxially 2-sulcate, usually not winged, occasionally slightly winged distally, the wings ca. 0.05 mm wide, densely covered by two kinds of scales and two kinds of hairs on both surfaces, the scales lanceolate, 1.5–3.2 × 0.15–0.3 mm, concolorous, brown, lustrous, twisted, bases truncate, cells of the scale body with thick walls, margins denticulate at base and short setiform projections toward the apex, apices acute (uniseriate), ca. 0.05 mm long, brown to reddish brown, the bullate scales

ca.  $2.3 \times 0.2$  mm, concolorous, brown, lustrous, twisted, bases rounded, cells of the scale body with thick walls, margins entire, apices long-filiform (multiseriate), the catenate hairs 0.4–2.0 mm long, brown, twisted, apices rounded, clavate hairs 0.1–0.15 mm long, reddish brown, apices rounded; **pinnae** 0.5–1.2  $\times$  0.3–0.6 cm, lanceolate, congested, 11–20 pairs, usually alternate, almost sub-opposite at base, patent, apices recurved; **secondary rachises** adaxially glabrous, abaxially with scales, catenate and clavate hairs similar to those of the rachises; **pinnules** entire, pinnatisect to pinnate, with two or three pairs of lateral veins, veins alternate, simple or furcate; **laminar tissue** reduced, 0.05–0.15 mm wide on each side of the secondary rachis, 0.1–0.2 mm wide on each side of the costule; **ultimate segments** with entire margins, apices usually rounded, sometimes acute; **sterile segments** 0.2–0.5 mm wide; **fertile segments** 0.4–0.5 mm wide. **Sori** 4–16 per pinna, usually immersed in the laminar tissue, rarely prominent, borne on acroscopic and basiscopic bases of the proximal and distal segments; **indusia** fragile, cyatheoid, 0.4–1.0 mm long, margins denticulate-lobed, sometimes slightly lacerate; **spores** 64 per sporangium, 58–63  $\mu$ m in diam., brown, surface finely rugate and aperture conspicuous.

*Distribution and ecology.*—*Cyathea minima* occurs in the boundary between Brazil (Roraima) and Venezuela (Amazonas), in the tepuis of Roraima Mount and “Pico da Neblina.” In these tepuis it grows in herbaceous-shrub forests, next to marshy savannas, between the outcrops of sandstone, in the fissures of the rocks; 1950–2597 m elev.

*Additional specimens examined.*—VENEZUELA. [Amazonas] Cerro de la Neblina, Venezuelan-Brazilian frontier, planicie de Zuloaga, Río Titirico, [01°04'N, 66°09'W], 2300 m, 10–15 Oct 1970, J.A. Steyermark 103891 (NY *p.p.*, US).

BRAZIL. **Roraima**: Parque Nacional do Monte Roraima, caverna próxima à trilha em direção a tríplice fronteira, 05°11'05"N, 60°44'21"W, 2597 m, 16 Aug 2016, S. Maciel & P.L. Viana 1854 (SP); idem, trilha próxima ao acampamento Quati, 05°12'38"N, 60°43'52"W, 2551 m, 19 Aug 2016, S. Maciel & P.L. Viana 1874 (SP).

*Etymology.*—The specific epithet refers to the size of the leaves of this species.

*Cyathea minima* is similar to *C. dejecta* and *C. indefinita* by the 4-pinnate-pinnatisect laminae and the cyatheoid indusia. *Cyathea dejecta* differs by its longer leaves (5.0–21.0 cm vs. 3.0–7.5 cm in *C. minima*; Fig. 19H), usually narrow-lanceolate (vs. lanceolate; Fig. 19H), and rachises with one kind of scales (lanceolate) and two kinds of hairs (catenate and clavate) (vs. two kinds of scales (lanceolate and bullate) and two kinds of hairs (catenate and clavate)).

The difference between *C. minima* and *C. indefinita* are discussed under the latter species.

11. *Cyathea pseudoctenitoides* S. Maciel & J. Prado, **sp. nov.** TYPE: VENEZUELA. **Amazonas**: Atabapo, Cerro Marahuaca-FHUIF, cumbre, altiplanicie de rocas expuestas, escabrosa, río abajo, 03°35'N, 65°20'W,

2330–2470 m, 3–4 Feb 1982, J.A. Steyermark, M. Guariglia, N. Holmgren, J. Luteyn & S. Mori 126091 (holotype: US barcode US00785471!; isotypes: NY barcode NY02713279!, MO, not seen) (Figs. 13F–K, 21E, 22).

**Diagnosis.**—*Cyathea pseudoctenitoides* is recognized by the sparse lamina, with ascending pinnae, rachises with one kind of scale (lanceolate) and two kinds of hairs (catenate and clavate) on both surfaces. In addition, it has broadly lanceolate rhizome scales ( $3.0\text{--}8.0 \times (0.3\text{--}) 0.5\text{--}1.2$  mm), opaque, bases rounded, cells of the scale body with thick walls, margins denticulate at base and short setiform projections toward the apex, the apices acute (uniseriate), 0.1–0.2 mm in long, reddish brown.

**Plants** rupicolous. **Rhizomes** erect, 3.2–4.0 mm diam. (5.0–25.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales  $3.0\text{--}8.0 \times (0.3\text{--}) 0.5\text{--}1.2$  mm, concolorous, brown to reddish brown, opaque, broadly lanceolate, slightly twisted at apex, bases rounded, sometimes truncate, cells of the scale body with thick walls, margins denticulate at base, short setiform projections toward the apex, apices acute (uniseriate), 0.1–0.2 mm long, reddish brown. **Leaves**  $9.3\text{--}21.5 \times 2.0\text{--}4.5$  cm, caespitose, erect; **petioles** stout, 0.8–2.4 mm diam., 2.0–7.0 cm long, dark brown to dark purple, semi-cylindrical, abaxially rounded, adaxially sulcate, proximal and distal portions with scale similar to those rhizomes, narrower, twisted; **laminae**  $6.3\text{--}14.0 \times 2.0\text{--}4.5$  cm, 4-pinnate-pinnatisect at base, 3- or 4-pinnate-pinnatisect distally, lanceolate, sparse, proximal pinnae gradually reduced, distal pinnae reduced, proximal segments overlapping the rachis; **rachises** abaxially rounded, adaxially 2-sulcate, not winged at base, slightly winged distally, the wings 0.05–0.1 mm wide, covered by one kind of scale and two kinds of hairs on both surfaces, the scales  $1.0\text{--}3.5 \times 0.15\text{--}0.25$  mm, concolorous, brown, lustrous, linear-lanceolate, twisted, bases truncate, cells of the scale body with thick walls, margins with long setiform projections at base and short projections toward the apex, apices filiform (multiseriate), the catenate hairs 0.4–1.8 mm long, brown, twisted, apices acute or rounded, the clavate hairs 0.1–0.3 mm long, reddish brown, straight, apices rounded; **pinnae**  $1.0\text{--}2.2 \times 0.6\text{--}1.0$  cm, lanceolate, sparse, 15–21 pairs, alternate, mostly ascending; **secondary rachises** with catenate and clavate hairs similar to those of the rachis on both surfaces, sometimes adaxial surface glabrescent; **pinnules** entire, pinnate to pinnatisect, two or three pairs of lateral veins, veins alternate, simple or furcate; **laminar tissue** reduced, 0.05–0.1 mm wide on each side of the secondary rachis, 0.05–0.3 mm wide on each side of the costule; **ultimate segments** with entire to sub-entire margins, apices usually acute, sometimes rounded; **sterile segments** 0.2–0.7 mm wide; **fertile segments** 0.4–0.6 mm wide. **Sori** 3–28 per pinna, usually prominent in the laminar tissue, rarely immersed, borne on the acroscopic and basiscopic bases of the proximal and distal segments, sometimes along of the entire pinna; **indusia** robust, cyatheoid, 0.9–1.4 mm long, margins denticulate-lobed, sometimes slightly or deeply lacerate; **spores** 64 per sporangium, ca. 53  $\mu\text{m}$  in diam., yellowish, surface rugate and aperture conspicuous.

*Distribution and ecology.*—*Cyathea pseudoctenitoides* occurs in northern Brazil (Roraima), Guyana (Cuyuni-Mazaruni), and Venezuela (Amazonas and Bolívar). It usually grows on rocky plateaus of open areas, along ravines, cliffs, edges of caves, beneath rocks, mainly in cracks and fissures of rocks; 1920–2810 m elev.

*Additional specimens examined.*—VENEZUELA. **Amazonas:** Atabapo, Cerro Marahuaca cumbre, sección noroccidental, 03°30'N, 65°26'W, 2500 m, 16 Feb 1981, *J.A. Steyermark et al. 124361 p.p.* (NY, RB); idem, cumbre, parte aislada al Sur-Oeste del cerro, 03°30'N, 65°20'W, 2450 m, 9–10 Feb 1982, *J.A. Steyermark et al. 126349* (US); idem, cumbre extremo noreste, 03°50'N, 65°28'W, 2580–2600 m, 30 Mar–1 Apr 1983, *J.A. Steyermark & F. Delascio 129223* (US); idem, summit on SE corner, 03°37'N, 65°21'W, 2700 m, 13–14 Oct 1988, *R. Liesner 24722 p.p.* (NY); idem, summit, SW side of center, 03°39'N, 65°26'W, 2660 m, 24 Oct 1988, *R. Liesner 25279* (US); idem, cumbre, sección suroriental, vecindades del zanjón, 03°37'N, 65°21'W, 2685 m, 15 Jan 1981, *B. Maguire et al. 65663* (NY). **Bolívar:** Chimantá Massif, central section, rocky slopes of zanjón bordering upper falls of Río Tirica above summit camp, [05°18'N, 62°03'W], 1950 m, 7 Feb 1955, *J.A. Steyermark & J.J. Wurdack 550* (NY); idem, east-central portion of summit of Apacará-tepui, [05°25'N, 62°11'W], 2450–2500 m, 21–22 June 1956, *J.A. Steyermark 75855, 75949* (NY); Piar, Macizo del Chimantá, sector SSE altiplanicie sur-oriental del Acopán-tepui, cabeceras del Río Arauac, 05°11'N, 62°00'W, 1920 m, 14–16 Feb 1984, *J.A. Steyermark et al. 130000* (NY); Summit of Mount Roraima, on northwest portion north and northwest of summit camp [05°12'N, 60°44'W], 2620–2740 m, 2 Sep 1944, *J.A. Steyermark. 58819* (NY); Summit of Mount Roraima, on southern half of the summit between summit camp, great central rift, central swamp, and pond at southern end, [05°09'N, 60°43'W], 2700–2740 m, 28 Sep 1944, *J.A. Steyermark 58875 p.p.* (NY, US); Cerro Roraima, cumbre, parte noreste da Venezuela inmediata al sur del hito que marca los limites com Guyana, Brasil y Venezuela, 05°12'N, 60°42'W, 2750–2800 m, 26 Aug–2 Sep 1976, *J.A. Steyermark et al. 112442* (NY), *112514-A* (NY), *112514* (NY, US); Roscio, vertiente Norte de la cumbre del Cerro Roraima, 05°15'N, 62°40'W, 2810 m, 27 Mar 1984, *G. Aymard & J. Luteyn 2503* (NY).

GUYANA. [**Cuyuni-Mazaruni**]: Summit Roraima, [05°12'N, 60°44'W], 8600 ft. [2621 m], s.d., *G.S. Jenman s.n.* (NY).

BRAZIL. **Roraima:** Parque Nacional do Monte Roraima, caverna próxima à trilha em direção a tríplice fronteira, 05°11'05"N, 60°44'21"W, 2597 m, 16 Aug 2016, *S. Maciel & P.L. Viana 1858* (SP); idem, entorno do Lago Gladys, 05°14'24"N, 60°44'12"W, 2555 m, 17 Aug 2016, *S. Maciel & P.L. Viana 1862, 1863, 1866* (SP); idem, id., floresta nebulosa paredão rochoso, 05°09'52"N, 60°47'01"W, 2000 m, 20 Aug 2016, *S. Maciel & P.L. Viana 1878* (SP).

*Etymology.*—The epithet “*pseudoctenitoides*” (pseudo = false) refers to the similarity of this species with *C. ctenitoides*.

*Cyathea pseudoctenitoides* resembles *C. ctenitoides* by the 4-pinnate-pinnatisect laminae. However, *C. ctenitoides* is recognized by the congested laminae, patent pinnae with recurved apices (vs. sparse laminae, ascending

pinnae, with ascending apices in *C. pseudoctenitoides*; Fig. 13F), long, linear rhizome scales, with entire margins, rarely with short setiform projections toward the apex (vs. scales broadly lanceolate, with denticulate margins at base and short setiform projections toward apex; Fig. 13G). The rachises have two kinds of scales, lanceolate and arachnoid (vs. all scales linear-lanceolate; Fig. 13I).

12. *Cyathea tatei* S. Maciel, R. Y. Hirai & J. Prado, **sp. nov.** TYPE: VENEZUELA. [Bolívar]: Mount Roraima, summit, [05°12'N, 60°44'W], 28 Nov 1927, G.H.H. Tate 445 (holotype: NY barcode NY02566194!; isotype: US barcode US00703399!) (Figs. 16G–L, 21F, 23).

*Diagnosis.*—*Cyathea tatei* is recognized by the laminae triangular-lanceolate, sparse, with proximal pinnae slightly reduced. The leaves are generally robust, (9.0–)28.0–40.0 × (2.2–)3.5–9.0 cm, rachises covered with two kinds of scales, arachnoid and lanceolate, and two kinds of hairs, catenate and clavate, on both surfaces, pinnae up to 4.5 cm long, secondary rachises on both surfaces scaly and pubescent, and indusia cyatheoid.

**Plants** rupicolous. **Rhizomes** erect, 2.2–4.4 mm diam. (5.6–12.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 2.0–5.0 × 0.2–0.5 mm, concolorous, paleaceous, opaque, lanceolate, twisted, bases truncate, cell of the center of the scale body with thick walls, margins entire, with short setiform projections toward the apex, apices acute (uniseriate), 0.5–0.1 mm long, hyaline. **Leaves** (9.0–)28.0–40.0 × (2.2–)3.5–9.0 cm, caespitose, erect; **petioles** stout, (0.5–)1.4–2.8 mm diam., (2.3–)12.0–15.0 cm long, dark brown to dark purple, semi-cylindrical, abaxially rounded, adaxially sulcate, proximal and distal portion with scales similar to those of the rhizomes, narrower, twisted; **laminae** (6.8–)16.8–25.0 × (2.2–)3.5–9.0 cm, 5- or 4-pinnate-pinnatisect at base, 3- or 4-pinnate-pinnatisect distally, triangular-lanceolate, sometimes broadly lanceolate, sparse, proximal pinnae slightly reduced, distal pinnae reduced, proximal segments overlapping the rachis; **rachises** abaxially rounded, adaxially 1- or 2-sulcate, not winged, sometimes slightly winged distally, the wings ca. 0.05 mm wide, covered with two kinds of scales and two kinds of hairs on both surfaces, the lanceolate scales 1.2–2.5 × 0.2–0.3 mm, concolorous, brown, lustrous, twisted, bases rounded with the center dark brown, cells of the scale body with thick walls, margins denticulate at base and short setiform projections toward the apex, apices acute (uniseriate), ca. 0.1 mm long, brown to reddish brown, the arachnoid scales 0.5–1.3 × 0.1–0.2 mm, concolorous, brown, lustrous, not twisted, bases truncate, cells of the scale body with thick walls, margins entire, apices acute (uniseriate), 0.05–0.1, reddish brown, the catenate hairs 0.5–1.5 mm long, brown, twisted, apices rounded, the clavate hairs 0.1–0.2 mm long, reddish brown, apices rounded; **pinnae** (1.0–)2.5–4.5 × (0.5–)1.0–2.5 cm, triangular-lanceolate, sometimes lanceolate, sparse, 12–28 pairs, alternate, usually ascending; **secondary rachises** with scales and catenate and clavate hairs similar to those of the rachises, on both surfaces, sometimes glabrescent

adaxially; **pinnules** entire, pinnate to pinnatisect, two or four pairs of lateral veins, veins alternate, simple or furcated; **laminar tissue** reduced, 0.05–0.2 mm wide on each side of the secondary rachis, 0.1–0.3 mm wide on each side of the costule; **ultimate segments** with entire margins, apices usually acute, sometimes rounded; **sterile segments** 0.2–0.5 mm wide; **fertile segments** 0.2–0.6 mm wide. **Sori** 4–34 per pinna, usually prominent in the laminar tissue, rarely immersed, borne on the acroscopic and basiscopic bases of the proximal and distal segments; **indusia** robust, cyatheoid, 0.6–1.0 mm long, margins usually sub-entire to sinuose, sometimes denticulate-lobed; **spores** 64 per sporangium, ca. 54  $\mu\text{m}$  in diam., yellowish, surface finely rugate and aperture conspicuous.

*Distribution and ecology.*—*Cyathea tatei* occurs in northern Brazil (Roraima), Venezuela (Amazonas and Bolívar), and possibly in Guyana. *Cyathea tatei* grows in large rocky outcrops in open areas, near wetlands and small bush forests, in nebular forests, on moist rocks, preferably in cracks of rocks; 2500–2700 m elev.

*Additional specimens examined.*—VENEZUELA. **Amazonas:** Atabapo, Cerro Marahuaca, summit on SE corner, 03°37'N, 65°21'W, 2700 m, 13–14 Oct 1988, *R. Liesner* 24722 (NY). **Bolívar:** Kukenán-tepui, summit, 05°13'N, 60°18'W, 2550 m, 12 Apr 1988, *R. Liesner* 23179, 23182 (NY).

[BRAZIL. **Roraima:** Monte] Roraima, [05°12'N, 60°44'W], 2500 m, Aug 1909, *E. Ule* 8502 (MG); idem, Parque Nacional do Monte Roraima, arredores da tríplice fronteira, 05°12'06"N, 60°44'15"W, 2583 m, 18 Aug 2016, *S. Maciel & P.L. Viana* 1870 (SP); idem, idem, floresta nebulosa próximo a um grande fosso “El fosso”, 05°11'56"N, 60°43'39"W, 2563 m, 18 Aug 2016, *S. Maciel & P.L. Viana* 1871, 1872, 1873 (SP); idem, trilha próxima ao acampamento Quati, 05°12'38"N, 60°43'52"W, 2551 m, 19 Aug 2016, *S. Maciel & P.L. Viana* 1875 (SP).

*Etymology.*—The specific epithet honors George H.H. Tate, who collected the type specimen.

The specimens treated here as *C. tatei* were treated as *C. dejecta* by Smith (1930) and White and Turner (2017). However, *C. dejecta* differs by the narrow-lanceolate laminae (vs. triangular-lanceolate in *C. tatei*; Fig. 16G), pinnae patent with apices recurved (vs. usually ascending), and rachises with one kind of scales, lanceolate (vs. two kind of scales, arachnoid and lanceolate).

Some specimens (*Maciel & Viana* 1871, 1872, 1873, 1875) included here in the concept of this species are smaller (9.0  $\times$  2.2 cm) than typical individuals of *C. tatei*, which are generally larger (40.0  $\times$  9.0 cm). However, the other characters, such as shape of the laminae, indument, and indusia are in accordance with the circumscription established here for *C. tatei*.

13. *Cyathea tepuiana* Christenh., Phytotaxa 1: 41. 2009. *Hymenophyllopsis steyermarkii* Vareschi, Acta Bot. Venez. 1(2): 89. 1966, non Tryon (1972). TYPE: VENEZUELA. **Bolívar:** Chimantá Massif, Torono-tepui, between bluff camp and low promontory north of bluff camp, along west-facing



portion of Torono-tepui, [05°24'N, 62°00'W], 1600–1700 m, 5 June 1953, J.A. Steyermark 75644 (holotype: VEN, not seen; isotypes: F barcodes F0075728, F0075729, images!, NY barcode NY00038207! US barcode US00478875!) (Figs. 18E, F, 23, 24A–D).

**Plants** rupicolous. **Rhizomes** usually erect, sometimes suberect, 1.0–2.0 mm diam. (4.5–15.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome visible, the scales  $0.8\text{--}1.6 \times 0.2\text{--}0.3$  mm, concolorous, dark brown, lustrous, lanceolate, twisted, bases truncate, with the center blackish, cells of the scale body with thick walls, margins entire or rarely with short setiform projections toward the apex, apices acute (uniseriate), 0.1–0.15 mm long, brown. **Leaves**  $4.0\text{--}21.0 \times 0.5\text{--}4.5$  cm, caespitose, erect; **petioles** stout, 0.6–1.3 mm diam., 0.5–7.0 cm long, dark brown to dark purple, cylindrical, proximal and distal portions with scales similar to those of the rhizomes, narrower, twisted; **laminae**  $8.0\text{--}20.0 \times 0.5\text{--}4.5$  cm, 3-pinnate-pinnatisect at base, 2- or 3-pinnate-pinnatisect distally, lanceolate, congested, proximal pinnae reduced, distal pinnae reduced, proximal segments usually not overlapping the secondary rachis; **rachises** usually abaxially rounded and adaxially complanate, sometimes abaxially complanate and adaxially rounded, usually not winged proximally and distally or sometimes slightly winged, the wings 0.05–0.1 mm wide, glabrous on both surfaces; **pinnae**  $0.8\text{--}1.7 \times 0.5\text{--}1.3$  cm, lanceolate, congested, 8–18 pairs, alternate, ascending; **secondary rachises** inconspicuous, glabrous on both surfaces; **segments** entire, pinnatisect, with costules inconspicuous, one pair of lateral veins, veins alternate, simple or furcate; **laminar tissue** reduced, 0.05–0.2 mm wide on each side of the secondary rachis, 0.2–0.3 mm wide on the each side of the costule; **ultimate segments** with entire margins, apices usually acute, sometimes rounded; **sterile segments** 0.2–0.6 mm wide; **fertile segments** 0.3–0.6 mm wide. **Sori** 1–4 per pinna, usually prominent in the laminar tissue, rarely immersed, borne on the acroscopic and basiscopic bases of the proximal and distal segments, rarely along the entire pinnae; **indusia** robust, bivalvate, abaxial valve 0.6–1.0 mm long, adaxial valve 0.8–1.4 mm long, both usually with margins entire, sinuose, rarely denticulate-lobed; **spores** 32 per sporangium, 58–63  $\mu\text{m}$  in diam., brown to dark brown, surface rugate and aperture conspicuous.

*Distribution and ecology.*—*Cyathea tepuiana* occurs only in Venezuela (Amazonas, Bolívar) in the tepuis Auyán-tepui, Torono-tepui (Massif Chimantá), and Cerro Marahuaca. It grows on the edges of the cliffs, along the cliffs, in crevices of shaded rocks, on open rocky plateaus, on ravines, near streams, preferably on cliffs on the shaded side in contact with a steady splash of water from waterfalls; 1600–2685 m elev.

*Specimens examined.*—VENEZUELA. **Amazonas:** Atabapo, Cerro Marahuaca, cumbre, sección suroriental, vecindades del zanjón, 03°37'N, 65°21'W, 2685 m, 15 Jan 1981, B. Maguire et al. 65658 (NY); idem, cumbre, sección noroccidental, 03°30'N, 65°26'W, 2500 m, 16 Feb 1981, J.A. Steyermark et al. 124496 (NY); idem, Atuhua-Shiho, cumbre, parte aislada al sur-oeste del

cerro, 03°30'N, 65°20'W, 2450–2480 m, 9–10 Feb 1982, *J.A. Steyermark et al.* 126333 (NY); idem, cumbre, extremo noreste, 03°50'N, 65°28'W, 2580–2600 m, 30 Mar–01 Apr 1983, *J.A. Steyermark & F. Delascio* 129211 (NY); idem, cumbre, parte central de la meseta sur-este, al lado de una grieta, a lo largo de la Quebrada Yekuana, afluente del Río Negro, 03°40'30"N, 65°26'20"W, 2560 m, 10–12 Oct 1983, *J.A. Steyermark* 129513 (NY); idem, summit, SW side of center, 03°39'N, 65°26'W, 2660 m, 22 Oct 1988, *R. Liesner et al.* 25165 (NY); 24 Oct 1988, *R. Liesner* 25302 (NY). **Bolívar:** Auyán-tepui, en la parte superior, [05°55'N, 62°32'W], 2300 m, Apr 1956, *V. Vareschi & Foldats* 4960 (US); idem, cumbre de la parte norte de la sección sur (división occidental del cerro), arriba del salto Churún, arriba de “Second Wall” de arenisca, noreste del campamento norte del Río Churún, [05°55'N, 62°32'W], 1820 m, 13 May 1964, *J.A. Steyermark* 93863 (NY); idem, cumbre de la parte sur, meseta de piedra arenisca, entre “Oso Woods Camp” y “Libertador”, [05°55'N, 62°32'W], 2050–2300 m, 15 May 1964, *J.A. Steyermark* 93963 (NY).

*Cyathea tepuiana* has congested laminae and ascending pinnae (Fig. 24A). The rachises and secondary rachises are glabrous on both surfaces (Fig. 24C) and rhizome scales are minute ( $0.8\text{--}1.6 \times 0.2\text{--}0.3$  mm), lustrous, and dark brown with black center at base (Fig. 24B).

14. *Cyathea trichomanoides* Christenh., *Phytotaxa* 1: 41. 2009. *Hymenophyllopsis superba* Lellinger, *Mem. New York Bot. Gard.* 38: 3, fig. 1. 1984, non Domin (1930). TYPE: VENEZUELA. **Amazonas:** Cerro de la Neblina, Río Yatua, east escarpment slopes of caño grande below cumbre camp, [01°04'N, 65°53'W], 1100–1800 m, 26 Nov 1957, *B. Maguire, J.J. Wurdack & C.K. Maguire* 42250 (holotype: US barcode US00433258!; isotypes: NY barcode NY02056453!, UC barcode UC2015216, image!) (Figs. 18G, 23, 25A–E).

**Plants** rupicolous. **Rhizomes** erect, 2.2–2.4 mm diam. (5.2–12.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales  $2.0\text{--}7.0 \times 0.1\text{--}0.2$  mm, concolorous, brown to hyaline, lustrous, long, linear, twisted, bases truncate, cells of the scale body with thin walls, margins entire, with short setiform projections toward the apex, apices filiform (multiseriate). **Leaves** 8.0–32.0  $\times$  1.6–5.0 cm, caespitose, erect, arching; **petioles** stout, (0.3–)0.6–1.2 mm diam., 0.8–2.0 cm long, dark brown to dark purple, cylindrical, proximal and distal portions densely covered by scales and catenate hairs, the scales of the proximal portion similar to those of the rhizomes, distally with scales  $1.8\text{--}3.2 \times 0.05\text{--}0.15$  mm, concolorous, brown to hyaline, lustrous, linear, twisted, bases truncate, cells of the scale body with thick walls, margins entire, apex long-filiform (multiseriate), the catenate hairs 1.0–2.2 mm long, hyaline, twisted, apices acute, the clavate hairs 0.1–0.2 mm long, reddish brown, apices rounded; **laminae** 7.3–29.0  $\times$  1.6–5.0 cm, 4-pinnate-pinnatisect at base, 3-pinnate-pinnatisect distally, elliptic, proximal and distal pinnae gradually reduced, congested, proximal segments overlapping the rachis and secondary rachis; **rachises** rounded on both

surfaces, not winged at base, winged distally, the wings 0.1–0.2 mm wide, densely covered by scales hyaline and two kinds of hairs, catenate and clavate similar to those of the distal portion of the petioles on both surfaces; **pinnae** 2.0–3.5 × 0.7–1.0 cm, triangular-lanceolate, congested, 15–53 pairs, usually alternate, almost sub-opposite at base, patent; **secondary rachises** with catenate and clavate hairs similar to those of rachises; **pinnules** entire, pinnate to pinnatisect, one or two pairs of lateral veins, veins alternate, simple, usually furcate up two times; **laminar tissue** reduced, 0.05–0.2 mm wide on each side of the secondary rachis, 0.1–0.3 mm wide on each side of the costule; **ultimate segments** with entire margins, apices rounded to acute; **sterile segments** 0.4–0.7 mm wide; **fertile segments** 0.3–0.4 mm wide. **Sori** 2–30 per pinna, usually immersed in the laminar tissue, rarely prominent, borne on acroscopic and basiscopic bases of the proximal and distal segments; **indusia** fragile, bivalvate, adaxial valve 0.6–0.8 mm long, abaxial valve 0.3–0.6 mm long, both margins denticulate-lobed or deeply lacerate; **spores** 32 per sporangium, ca. 53 µm in diam., yellowish, surface with sparse rodlets and aperture inconspicuous.

*Distribution and ecology.*—*Cyathea trichomanoides* is known only from Venezuela (Amazonas, Río Negro), in Pico da Neblina and Cerro Aracamuni; it likely also occurs on the Brazilian side of Pico da Neblina. It grows near large patches of forests with moss-covered trees, on misty paths, along streams, in ravines, near the edge of the tepui, growing along the rock; 1100–1800 m elev.

*Specimens examined.*—VENEZUELA. **Amazonas:** Río Negro, Cerro de la Neblina, camp XI, 6.2 km NNE Pico Phelps (=Neblina) (20.5 km ENE Nebliat base camp), 00°51'45"N, 65°58'52"W, 1600 m, 28 Feb 1985, *J. Beitel 85314* (NY, US); Cerro Aracamuni, summit proa camp., 01°32'N, 65°49'W, 1400 m, 25 Oct 1987, *R. Liesner & G. Carvenali 22424* (NY).

*Cyathea trichomanoides* is easily recognized by the dense covering of catenate, hyaline and twisted hairs on the leaves (Fig. 25C). In addition, the proximal pinnae are gradually reduced (Fig. 25A), and the pinnae are patent (Fig. 25D).

According to White and Turner (2017), large plants of *C. trichomanoides* have four vascular bundles in the petiole, more than found in any other species of *Cyathea* clade *Hymenophyllopsis*.

15. *Cyathea universitatis* (Vareschi) Christenh., *Phytotaxa* 1: 41. 2009. *Hymenophyllopsis universitatis* Vareschi, *Acta Biol. Venez.* 2: 156, fig. 4. 1958. TYPE: VENEZUELA. **Bolívar:** plateau del Auyán-tepui, [05°55'N, 62°32'W], 2300 m, 20 Apr 1956, *V. Vareschi & E. Foldats 4938* (holotype: VEN, not seen; isotypes: US barcodes US0065655!, US00785442!) (Figs. 18H, 23, 25F–K).

**Plants** rupicolous. **Rhizomes** erect, 7.0–10.0 mm diam. (12.0–21.0 mm diam., including the roots, petioles, and scales), scaly, surface of the rhizome not visible, the scales 10.0–16.0 × 0.3–0.4 mm, concolorous, brown to ferruginous, lustrous, lanceolate, twisted, bases rounded, cells of the scale

body with thick walls, margins entire, apices filiform (multiseriate). **Leaves** 4.5–23.5 × 2.0–7.5 cm, caespitose, erect; **petioles** stout, 0.6–2.0 mm diam., 1.8–6.3 cm long, dark brown to dark purple, cylindrical, scales of the proximal portion similar to those of the rhizome, scales of the distal portion similar to those of rachises; **laminae** 3.5–18.6 × 2.0–7.5 cm, 3-pinnatisect at base, 2-pinnatisect distally, broadly lanceolate, sparse, proximal segments gradually reduced, distal segments reduced to gradually reduced, proximal segments not overlapping the rachis and costa; **rachises** rounded on both surfaces, sometimes complanate, winged, the wings 0.35–0.45 mm wide, with one kind of scales and two kinds of hairs, sparse on both surfaces, the scales 3.0–5.2 × 0.15–0.2 mm, concolorous, ferrugineous, lustrous, linear-lanceolate, twisted, bases truncate, cells of the scale body with thick walls, margins entire or with sparse setiform projections at base, apices filiform (multiseriate), the catenate hairs 0.6–1.5 mm long, twisted, hyaline, apices acute, the clavate hairs 0.1–0.25 mm long, straight, reddish brown, apices rounded; **segments** 1.6–4.0 × 0.4–1.0 cm, lanceolate, sparse, 9–27 pairs, with conspicuous costa, usually opposite, sometimes alternate, patent; **costae** inconspicuous, with sparse catenate and clavate hairs, similar to those of the rachises, on both surfaces; **ultimate segments** entire, pinnatisect, with costule inconspicuous, one pair of lateral veins, veins alternate, simple or furcate, margins entire, apices acute, sometimes rounded; **laminar tissue** broad, 0.4–0.6 mm wide on each side of the costa, 0.4–0.5 mm wide on each side of the costule; **sterile segments** 0.4–1.8 mm wide; **fertile segments** 0.8–1.2 mm wide. **Sori** 6–23 per segment, usually prominent in the laminar tissue, rarely immersed, borne usually on the acroscopic and basiscopic bases of the proximal and distal segments, rarely along the entire segment; **indusia** robust, cyatheoid, 0.9–1.6 mm long, margin sub-entire to sinuose, seldom denticulate-lobed; **spores** 32 per sporangium, ca. 53 µm in diam., hyaline, surface rugate (with rodlets) and aperture conspicuous.

*Distribution and ecology.*—*Cyathea universitatis* occurs in Venezuela (Bolívar) in the tepuis Auyán-tepui and Acopán-tepui (Massif Chimantá). It grows at shaded cave edges and humid cliffs, on large rocks or in the crevices of rocks; at high elevations 2050–2300 m.

*Specimens examined.*—VENEZUELA. **Bolívar:** Auyán-tepui, cumbre de la parte sur, meseta de piedra arenisca, entre “Oso Woods Camp” y “Libertador”, [05°55'N, 62°32'W], 2050–2300 m, 15 May 1964, *J.A. Steyermark* 93978 (NY); idem, al sur e inmediatamente debajo de “Libertador” hacia la escarpa superior, arriba de “El Peñón”, [05°55'N, 62°32'W], 2200 m, 17 May 1964, *J.A. Steyermark* 94041 (F, NY); idem, cumbre, sector suroriental, 05°42'N, 62°26'W, 2140 m, 23 Feb 1978, *J.A. Steyermark et al.* 116006 (US); idem, id., 26 Feb 1978, *J.A. Steyermark et al.* 116030 (US); Macizo del Chimantá. Acopán-tepui, [05°12'N, 62°04'W], Jun 1997, *P. Wolf* 756 (UC).

*Cyathea universitatis* is characterized by the 3-pinnatisect, sparse laminae (Fig. 25F) with long segments (1.6–4.0 cm long), with twisted lanceolate rhizome scales (Fig. 25G, H), rachises with one kind of scale (linear-lanceolate, Fig. 25I) and two kinds of hairs (catenate and clavate), on both surfaces, sori

generally prominent in the laminar tissue (Fig. 25J, K), and indusia cyatheoid (Fig. 25K).

*Cyathea universitatis* can be confused with *C. asplenioides*, which also has 3-pinnatisect laminae. However, *C. asplenioides* has narrow-lanceolate congested laminae (vs. broadly lanceolate and sparse in *C. universitatis*), shorter segments (0.5–3 cm long vs. 1.6–4 cm long), which are ascending (vs. patent), and rachises usually glabrous on both surfaces (vs. with scales and hairs on both surfaces).

*Cyathea universitatis* has only one vascular bundle at the petiole in adult plants (White and Turner, 2017).

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The new species described in the present paper appear in bolded italics in the list below.

1. *Cyathea alsophiloides* S. Maciel & Lehnert
2. *Cyathea asplenioides* (A. C. Sm.) Christenh.
3. *Cyathea ctenitoides* (Lellinger) Christenh.

4. *Cyathea cylindrica* S. Maciel & Lehnert
5. *Cyathea dejecta* (Baker) Christenh.
6. *Cyathea hymenophylloides* (L. D. Gómez) Christenh.
7. *Cyathea incognita* (Lellinger) Christenh.
8. ***Cyathea indefinita*** S. Maciel & J. Prado
9. *Cyathea lellingeriana* S. Maciel & J. Prado
10. ***Cyathea minima*** S. Maciel & J. Prado
11. ***Cyathea pseudectenitoides*** S. Maciel & J. Prado
12. ***Cyathea tatei*** S. Maciel, R. Y. Hirai & J. Prado
13. *Cyathea tepuiana* Christenh.
14. *Cyathea trichomanoides* Christenh.
15. *Cyathea universitatis* (Vareschi) Christenh.

INDEX OF SCIENTIFIC NAMES OF *CYATHEA*, CLADE *HYMENOPHYLLOPSIS*

The number between parentheses corresponds to the species number in the taxonomic treatment. Accepted names appear in bolded italics.

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*Asplenium dejectum* (Baker) Pittier (5)  
***Cyathea alsophiloides*** S. Maciel & Lehnert (1)  
*Cyathea asplenioides* (A. C. Sm.) Christenh. (2)  
***Cyathea ctenitoides*** (Lellinger) Christenh. (3)  
*Cyathea cylindrica* S. Maciel & Lehnert (4)  
*Cyathea dejecta* (Baker) Christenh. (5)  
***Cyathea hymenophylloides*** (L. D. Gómez) Christenh. (6)  
*Cyathea incognita* (Lellinger) Christenh. (7)  
*Cyathea indefinita* S. Maciel & J. Prado (8)  
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***Cyathea minima*** S. Maciel & J. Prado (10)  
***Cyathea pseudectenitoides*** S. Maciel & J. Prado (11)  
***Cyathea tatei*** S. Maciel, R. Y. Hirai & J. Prado (12)  
***Cyathea tepuiana*** Christenh. (13)  
***Cyathea trichomanoides*** Christenh. (14)  
***Cyathea universitatis*** (Vareschi) Christenh. (15)  
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*Hymenophyllopsis ctenitoides* Lellinger (3)  
*Hymenophyllopsis dejecta* (Baker) K. I. Goebel (5)  
*Hymenophyllopsis hymenophylloides* L. D. Gómez (6)  
*Hymenophyllopsis incognita* Lellinger (7)  
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